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Edited by

CARLETON REA and J. RAMSBOTTOM

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By E. J. Butler, C.I.E., F.R.S.

THE DEVELOPMENT OF ECONOMIC MYCOLOGY IN THE EMPIRE OVERSEAS.

In endeavouring to sketch the rise and development of economic mycology in the more distant parts of the Empire, the field to be covered is so vast that little more than a bare outline can be attempted. Much that one would have liked to treat in some detail has to be merely mentioned, and many matters of interest must be omitted. I have also had to impose some limitations on my theme or it would become altogether unwieldy, and if I say little of the English mycologists, Berkeley, Broome, Cooke, Massee, and others who did so much for the early study of the injurious fungi of the Empire, it is not that I am unmindful of their labours. Their work, however, was done in England, and I have endeavoured to confine myself, so far as possible, to the work actually done in the Dominions and Colonies themselves.

From the middle of the last century, there was a rapid growth in appreciation of the injury done to living plants by parasitic fungi. The calamity of the potato blight in the years following 1845 focussed attention on the terrible potentialities for harm of these organisms, and when from 1869 onwards the coffee plantations of Ceylon, on which the prosperity of that Colony mainly depended, were swept by disease, the lessons of the potato blight epidemic were still fresh in men's minds. Nevertheless, it was more than ten years before the appeals of the Ceylon planters for scientific assistance were met by the decision to send out a special investigator from home. Harry Marshall Ward, whose biological training was begun by Huxley at South Kensington and completed under Sachs at Würzburg, was appointed Government Cryptogamist for Ceylon in 1880, and sent out on a temporary mission to study the coffee leaf disease caused by *Hemileia vastatrix*, which by that time had caused a loss of some £15,000,000. He remained only two years, but in that brief period carried out one of the most complete, as it was the first, of the detailed studies of a disease of a tropical plantation crop caused by a fungus.

In 1887 Mr (afterwards Sir) Arthur E. Shipley was sent out on a special mission by the Colonial Office to investigate a disease of onions in Bermuda, the cause of which in a short time he elucidated as the fungal parasite, *Peronospora Schleideni*.

Ten years later the Ceylon planters were again faced with a serious disease in one of the crops—cacao—that had replaced

the now abandoned coffee. This time they took matters into their own hands and secured a scientific adviser for themselves. John Bennett Carruthers, the son of William Carruthers, the Keeper of Botany at the Natural History Museum, was appointed Cryptogamist to the Ceylon Planters' Association in 1897 and remained in Ceylon until 1899, a period during which he published a series of reports on cacao canker.

By this time, however, it was abundantly evident that these short tours by specially sent out men did not meet the needs of the rapidly growing agricultural industries of the overseas Empire, and as each Dependency founded a Government agricultural department the appointment of officers for the study of fungous diseases of plants became more and more common.

In this development Australia led the way. In 1890 Daniel McAlpine, who had arrived in Melbourne from Scotland six years previously to take up a lectureship in biology, was appointed Vegetable Pathologist to the Department of Agriculture, Victoria. This and the almost coincident appointment of Cobb to a similar post in New South Wales were, so far as I have been able to ascertain, the first whole-time appointments to permanent posts in applied mycology in the Government service of any Dominion or Colony. McAlpine, who is still living in retirement near Melbourne, was in all respects fitted to be a pioneer in the science of phytopathology in the daughter nations of the Empire. He had studied biology under Huxley and botany under Thiselton-Dyer at the Royal College of Science in London, before becoming a lecturer at the Heriot Watt College, Edinburgh, in 1877. Commencing work at a time when the influence of the great European masters, de Bary, the Tulasnes, Berkeley, and others, who had thrown such a flood of light on the causation of plant diseases through their studies of the parasites, was supreme, he built his foundations on a systematic basis. One of his first preoccupations was to compile a systematic census of Australian fungi, a work of great labour but a necessary preliminary to the identification of the parasites with which he had to deal. The list of Australian fungi that he published in 1895 was in no sense critical and has required much revision, but at least he learnt how little was known in many groups and how the smaller injurious forms had been neglected. Of the rusts, for instance, there are only eighty-one mentioned in the 1895 list, as against one hundred and sixty in the critical monograph that he published eleven years later. As a mycologist he is best known by this and the companion volume on Australian smuts published in 1910, both models of their kind; but in some thirty other papers he has added to the fungous flora of his adopted country in every group.

On the more definitely pathological side his three volumes on the diseases of citrus fruits (1899), of stone fruits (1902), and of potatoes (1911) are well known, and in a series of papers in the *Journal* of the Department of Agriculture, Victoria, and the Bulletins of the same Department, he has largely contributed to a knowledge of the fungous diseases of most of the crops grown in the temperate parts of Australia.

In 1911 he was put on special duty to investigate the nature and control of bitter pit of apples and in five monumental reports, published between 1912 and 1916, he has provided one of the most complete studies of any plant disease in existence. Whether his theories as to the causation of this condition will stand, it is as yet too soon to say, but they mark an ability to apply physiological considerations to the explanation of disease in plants which gives him a definite rank amongst the leading exponents of the modern school of phytopathology.

Nathaniel Cobb arrived in Australia, after studying in the United States, not long after McAlpine and was appointed as Vegetable Pathologist to the Department of Agriculture, New South Wales, at about the same time as the latter. Though in 1893 he published a *Host and Habitat Index of Australian Fungi*, his interests were more in the study of function than of structure and his aims were to discover what the parasites with which he worked did, rather than what they were. In his pamphlet on *Fungus Diseases of the Sugar-cane*, published in the same year, he gave the first description of the bacterial disease still often known as Cobb's disease of sugar-cane, which has since proved such a serious menace to this crop in Australia, Fiji, Porto Rico and elsewhere. He is also responsible for the name "Bitter Pit" applied to the disease that has attracted so much attention in all apple-growing countries, and in his "Letters on the Diseases of Plants," published in the *Agricultural Gazette of New South Wales* from 1897 to 1904, a large amount of information on the economic aspect of fungous diseases in Australia is contained. The campaign against rust in wheat, the lines of which were laid down in a series of annual interstate Conferences from 1891 to 1894 and which stands out as one of the most fruitful instances of the co-operation of scientific and practical men on record, had no more energetic supporter than Cobb. During this period, too, he commenced his studies of the nematode worms that attack plants, to which he became more and more attracted as time went on. In 1905 he was appointed Director of the Division of Pathology and Physiology at the Experiment Station of the Hawaiian Sugar Planters' Association and he remained in Honolulu until called to the Bureau of Plant Industry in Washington. In recent years he has abandoned mycology for

helminthology, but he ranks with McAlpine as one of the founders of plant pathology in the overseas parts of the Empire.

The third of the Australian pioneers was Henry Tryon, who, as Assistant Curator in the Queensland Museum, published a *Report on Insect and Fungus Pests* for the Department of Agriculture, Queensland, in 1887. Tryon was appointed Government Entomologist in the Department of Agriculture in 1894 or 1895 but continued to give advice on fungous diseases and was eventually made Entomologist and Vegetable Pathologist, a post which he still holds. He is responsible for some of the earliest records of destructive diseases, such as plum rust, in Australia, but his preoccupation with his entomological duties prevented his giving much time to mycology or plant pathology.

The other States in the Australian Commonwealth were considerably later in developing but have all provided for mycological and plant pathological investigations in one form or another, usually through specially appointed officers in their Departments of Agriculture. The chief contribution to knowledge of the Tasmanian fungi has been made by Leonard Rodway, the Government Botanist, who is one of the leading systematic mycologists of Australasia. Altogether there are now some fifteen members of the various agricultural departments more or less directly concerned with economic mycology in the Commonwealth, and recently a senior mycologist, Dr B. T. Dickson, has been appointed by the Commonwealth Council of Science and Industry to co-ordinate their work.

In 1908 a Government Bureau of Microbiology was established in New South Wales and for some years a considerable amount of work on plant diseases was carried out by members of its staff, especially T. Harvey Johnston and George P. Darnell-Smith. This ceased when the latter became Biologist to the Department of Agriculture.

Outside the Government departments important work on the fungous flora of the continent has been done by Dr J. Burton Cleland of the medical faculty of Adelaide University who, with E. Cheel, the Curator of the National Herbarium at Sydney, has greatly extended knowledge of the higher fungi of Australia, while Miss Ethel McLennan of Melbourne University is doing the same for the Ascomycetes. In plant pathology, too, the Universities are beginning to play an important part, the recent brilliant elucidation of the nature of bunchy top disease of bananas having been greatly aided by the University of Queensland, while Waterhouse and others of Sydney University have investigated cereal diseases. The Colonial Sugar Refining Company have in D. S. North, their privately employed pathologist, one of the leading sugar-cane pathologists of the day.

In the sister Dominion of New Zealand, Thomas W. Kirk, who was Government Biologist in the Department of Agriculture from 1893 to 1909, published a number of Leaflets and Bulletins dealing in popular language with the common diseases of plants in the country. At the same time he collected extensively, and many of the New Zealand fungi determined in England were obtained from him. In 1904 A. H. Cockayne became Assistant Biologist, and to this designation was added that of Vegetable Pathologist in 1908. Cockayne continued the series of popular articles on fungous diseases in which he had previously collaborated with Kirk, when he succeeded the latter as Biologist in 1909. It was not, however, until after the war that a mycologist was appointed, Gordon Herriot Cunningham becoming the first Government Mycologist in New Zealand. In the brief period which has since elapsed he has devoted himself with extraordinary energy to the study not only of the plant diseases but also of the fungous flora of the Dominion. A series of papers on various fruit diseases published in New Zealand journals was succeeded by a book on the *Fungous Diseases of Fruit Trees*, published in 1925, which has gained for the author a high reputation as a pathologist outside his own country. On the systematic side he has produced monographs of the rusts, smuts, Nidulariales, and *Cordyceps* of New Zealand and critical revisions of a large part of the Gasteromycetes of Australasia, besides developmental studies of several species of this group. At the present time there are two other officers in the biological branch of the New Zealand Department of Agriculture engaged with Cunningham in the study of plant diseases and, in addition, the privately endowed Cawthron Institute of Scientific Research has, as Mycologist, Dr Kathleen Curtis, whose work on potato wart disease is well known.

I have already mentioned that J. B. Carruthers was Cryptogamist to the Ceylon Planters' Association from 1897 to 1899. He returned in 1900 as Government Mycologist and Assistant Director of the Royal Botanic Gardens, Peradeniya, a post which he held until 1905. During this period he continued his work on cacao diseases and commenced the study of those of tea and rubber. In 1905 he was appointed the first Director of the newly created Department of Agriculture in the Federated Malay States and after a vain attempt to combine mycology with administration obtained the services of a whole time Mycologist in William Gallagher, in 1907. He was thus the first of the line of official mycologists in Ceylon and the Federated Malay States, to whom so much of our knowledge of the diseases of tea, rubber, cacao, and coconuts is due.

In Ceylon, Carruthers was succeeded as Government Myco-

logist by Thomas Petch, who became Botanist and Mycologist to the Department of Agriculture when that Department was founded some years later. For twenty years Petch laboured in the Ceylon Department, studying the fungous flora of the island and the diseases of the two great plantation crops, tea and rubber, which are the main sources of its prosperity. As a result, there is no single part of the British Empire overseas the fungi of which are better known, while in the two volumes on the diseases of *Hevea* rubber and of the tea plant we have the most complete studies of the pathology of single tropical plantation crops in existence. These form only a part of his work. The series of papers on entomogenous fungi that he has contributed to the pages of the *Transactions* of this Society are too well known to need more than mention, and in numerous other contributions he has dealt with critical questions of the morphology and systematic position of a whole series of tropical fungi.

As the work of the Ceylon mycological section expanded, its staff was enlarged. Two assistant mycologists were added to it after the war, besides a group of trained junior assistants recruited locally and in India; while during the same recent period the development of legislative measures for the control of diseases and pests and the general sanitation of crops led to the appointment of Plant Pests Inspectors in the Agricultural Department, working in close collaboration with the mycological and entomological divisions, and including in their ranks several trained and keen mycologists. This latest development of economic mycological work in the Colonies will be referred to more fully later on.

In 1925 Petch retired from Government Service, being succeeded by William Small from Uganda, and shortly after he was appointed Director of the new Tea Research Institute of Ceylon, an institution controlled largely by the planters themselves. Some years previously the rubber industry had provided for its own special needs by the establishment of a rubber research scheme by the Rubber Growers' Association. Under this scheme the Association employs its own mycologist, independently of the staff of the Department of Agriculture.

We have already seen that Carruthers lost no time in developing a mycological branch in the new Agricultural Department of the Federated Malay States. The history of this branch is, however, widely different from that in Ceylon. The extraordinary wave of prosperity that swept over Malaya and the Dutch East Indies as a result of the tremendous growth in the demand for rubber led to a fierce competition between the industry and Government Departments for the services of com-

petent scientific men. Gallagher, after succeeding Carruthers as Director in 1909, resigned a year later to become technical adviser to a large rubber company in Sumatra, and was followed as Director by still a third mycologist in Lewton-Brain, whom we shall find was one of the early mycologists in the West Indies. Keith Bancroft was appointed Mycologist in 1910 and resigned in 1913. E. Bateson was appointed Assistant Mycologist in 1911 and resigned in 1914, being subsequently appointed Mycologist and Agricultural Adviser to the Chartered Company of British North Borneo. F. T. Brooks acted as Mycologist with A. Sharples as assistant in 1914, and the latter became chief of the branch soon afterwards. W. N. C. Belgrave entered in 1914 as assistant, but had charge of the branch in Sharples's absence on war service. From 1911 onwards there were three mycological posts in the sanctioned cadre of the Department, but they were seldom all filled at the same time and there were constant changes of personnel. Since the war Sharples has remained in charge, with two assistants.

While the Government Department was struggling to meet the mycological needs of the Malay Peninsula, the rubber industry began to appoint mycologists for its own special requirements. During the war there were six mycologists working in private employment for bodies like the Rubber Growers' Association, the Malay Peninsula Agricultural Association, and companies like the Société Financière des Caoutchoucs. As there was little co-operation either with the Government Department or amongst themselves, there was much overlapping and waste of effort; the recent foundation of the Rubber Research Institute of Malaya jointly by the Government and the planters themselves, and with its own staff of mycologists adequate for the needs of the industry with James Weir, formerly of the United States Department of Agriculture, at their head, can be directly traced to this cause.

As an inevitable result of the want of continuity in the work in Malaya, the development of economic mycology there has been markedly different from that in Ceylon. Each officer when appointed found himself confronted with one or another of the successive outbreaks of disease that have afflicted the rubber plantations. Attention was focussed as a rule on single problems, and the bulk of the work done in Malaya has been the monographic study of individual diseases and their control. Each of the mycologists mentioned has carried out detailed research into the cause and control of one or more of the chief diseases of rubber, and our knowledge of the pathology of the rubber tree is very largely based on their work. None has had time to undertake a general survey of the parasitic and other fungi of

the country and except for a List of the Fungi of the Malay Peninsula compiled in 1921 by T. F. Chipp, Assistant Director of the Singapore Botanic Gardens, and a few other smaller lists, little has as yet been done to gain a knowledge of the fungi of Malaya. Chipp's list, for instance, contains only seven species each of rusts and smuts and nearly two-thirds of the fungi recorded are Basidiomycetes.

One other development in Malaya deserves mention. This is the formation in 1913 of an Inspection Division of the Department of Agriculture charged with the general supervision of the sanitation, mainly from the point of view of insect pests and fungous diseases, of the plantations. F. W. South, then Mycologist in the Imperial Department of Agriculture in the West Indies, was appointed Chief Inspector, with four assistants, a number subsequently increased to keep pace with the growth of the plantation industry. These officers are responsible for the administration of the various plant pest and disease laws as well as the advising on all matters connected with the routine prevention and control of plant diseases. Similar staffs are now found in several parts of the Empire: Jamaica has no less than eighteen Inspectors of Plant Diseases (mainly for the control of Panama disease of bananas), the Gold Coast has about fourteen Inspectors of Plantations for cacao sanitation, Ceylon has three Inspectors for Plant Pests and Diseases, and there are similar officers elsewhere. It is obvious that the presence of a separate staff for such purposes sets free the research officers from much work of a routine nature.

Mycological development in the West Indies as elsewhere was slow and gave few results of permanent value until the appointment of whole time officers in the agricultural service. The Imperial Department of Agriculture for the West Indies was established in 1898 with Mr, afterwards Sir Daniel, Morris at its head. In the following year Albert Howard went out from Cambridge as Lecturer in Agricultural Science in Barbados, and in 1900 he was appointed acting Mycologist and Agricultural Lecturer in the Imperial Department. In his brief period as a mycologist he worked on the diseases of cacao and sugar-cane, his work on the latter crop (in which he was instrumental in establishing the real cause of the terrible rind disease which between 1895 and 1900 threatened the very existence of the sugar plantations) being best known. In 1902 he left to take up the position of Economic Botanist in the Indian Department of Agriculture and was succeeded by Lawrence Lewton-Brain, who also only spent a few years in the West Indies, leaving in 1905 to join Nathaniel Cobb as Assistant Director in Honolulu, whence, as we have already seen, he went to Malaya to succeed

Gallagher in 1910. Lewton-Brain continued Howard's work on sugar-cane and cacao and also studied cotton diseases. He was succeeded by Frank Arthur Stockdale, who remained for four years before becoming Assistant Director of the Department of Science and Agriculture and Government Botanist, British Guiana, in 1909. Like Lewton-Brain, Stockdale after some work on the diseases of coconut and cacao soon abandoned mycology for an administrative career, becoming Director of Agriculture in Mauritius in 1912 and in Ceylon in 1916. F. W. South followed Stockdale as Mycologist and Agricultural Lecturer and like him remained for four years before proceeding to Malaya in 1913 as already mentioned. South was succeeded by William Nowell, the post of Agricultural Lecturer ceasing to be combined with that of Mycologist from 1915. Between 1913 and 1920 Nowell carried out a number of important researches on the diseases of limes, cacao, cotton, and coconuts and when appointed in the latter year Assistant Director of the Department of Agriculture in Trinidad and Tobago he continued his studies on plant diseases both independently and in collaboration with his successor, S. F. Ashby. In 1923 he published his book on the *Diseases of Crop Plants in the Lesser Antilles*, a work which has secured him a position in the front rank of vegetable pathologists. In 1926 Nowell was appointed Director of the Amani Research Institute in East Africa, on its revival after a period of stagnation following its capture from the Germans in 1915.

While this development in the Imperial Department was going on, some of the more important of the West Indian islands appointed mycologists of their own. In 1909 James Birch Rorer was made Mycologist to the Board of Agriculture, Trinidad. Rorer came from the United States, where he had worked with Erwin F. Smith at a time when the latter was much preoccupied with the bacterial diseases of plants, and very soon after his arrival in Trinidad he described two such diseases, the so-called "Moko" disease of bananas and the bud rot of coconuts. The first of these he attributed to *Bacillus Musae*, an organism which Ashby has recently shown to be identical with *Bacterium solanacearum*. In regard to coconut bud rot he had accompanied Smith in 1904 on a visit to Cuba to investigate this disease and he accepted the conclusion of Smith and Johnston that *B. coli* was the cause, a conclusion not substantiated by subsequent work. Later on he did much work on the green muscardine disease of the sugar-cane frog-hopper insect and on various fruit diseases. His most important discovery, however, was that the cause of cacao canker, which Carruthers, Massee, Howard, and others had attributed to a *Nectria*, was in reality

a *Phytophthora*, and he made the first detailed study of one of the several major diseases of tropical crops caused by the organism generally known as *P. Faberi*. In 1911 Rorer published a Preliminary List of Trinidad fungi, the only one of the kind contributed by any of the mycologists in the British West Indies, no doubt because few had remained long enough to get to know the fungi of these islands. In 1917 Rorer left the West Indies to take up private employment as mycologist to an association of cacao growers in Ecuador, being succeeded in Trinidad by F. Stell.

In 1906, the Department of Agriculture in Jamaica appointed Sydney Francis Ashby as Fermentation Chemist and Bacteriologist, to work mainly on the microbiology of the rum fermentation industry of the island. Ashby came from Rothamsted with, like Rorer, a special knowledge of bacteriological technique, which he was afterwards to apply to plant pathogens. In 1912 he was appointed Microbiologist, and the study of plant diseases was added to his previous duties. This post he held until he became Mycologist in the Imperial Department in succession to Nowell in 1921. During this period he made important contributions to knowledge of the diseases of bananas, sugar-cane and coconuts and subsequently, on his appointment as Professor of Mycology in the newly established Imperial College of Tropical Agriculture in Trinidad in 1922, he continued the studies of the genus *Phytophthora* which had developed from his investigations on coconut diseases, and joined Nowell in a detailed study of the curious group of yeast-like fungi associated with fruit diseases of cotton and other plants.

In 1921 the Board and Department of Agriculture, Bermuda, employed the well known American pathologist, H. H. Whetzel, to study the plant diseases of Bermuda during a period of vacation from his duties at Cornell University, and he paid a return visit in 1923. Whetzel's recommendations led to the appointment of Lawrence Ogilvie as Plant Pathologist for Bermuda in 1923. In the same year R. A. Altson was appointed Assistant Botanist and Mycologist to the Department of Science and Agriculture, British Guiana. Besides the Professor of Mycology in the Imperial College there are now, therefore, mycologists in Trinidad, Jamaica, British Guiana, and Bermuda.

Following on the mycological appointments in Ceylon and the West Indies, in 1900 the Government of India decided to appoint a Cryptogamic Botanist mainly for the study of the diseases of plants, and the writer was sent out to India early in 1901. Posted at first to the Botanical Survey of India with headquarters in the Royal Botanic Gardens, Calcutta, he was soon after transferred to the newly founded Imperial Depart-

ment of Agriculture and moved to Dehra Dun. When the Agricultural Research Institute at Pusa was built in 1905 he was appointed a member of its staff, and his designation was changed to Imperial Mycologist in the following year. In 1908 William McRae was appointed Second Imperial Mycologist at Pusa, and on his transfer to the newly established post of Government Mycologist, Madras, he was succeeded by F. J. F. Shaw in 1910. In 1919 a third mycologist was added to the mycological section at Pusa, Jehangir Fardunji Dastur becoming Supernumerary Mycologist after nine years as senior assistant in the section. Some six or seven junior assistants recruited locally were also at work during most of this period.

Later on mycologists were added to the Agricultural Departments of some of the other provinces, as well as professors of mycology in some of the Agricultural Colleges, mostly locally recruited men, trained at Pusa. The Indian Cotton Committee have a special mycologist for cotton. The Departments of Agriculture in some of the native States have also appointed similar officers. Leslie Coleman went out from Canada, after a period of study in Washington and Berlin, as Mycologist and Entomologist to the Government of Mysore in 1908, and carried out a series of valuable researches on diseases of areca palms, coffee, and sandal-wood, maintaining his interest in plant pathology after his appointment as Director of Agriculture in Mysore some years later.

Independently of the Government Departments the great tea industry of India founded a scientific department in 1900, and several of the early scientific officers of this department concerned themselves with the diseases of the tea bush. In the *Pests and Blights of the Tea Plant,* George Watt and Harold H. Mann included most of what was known on the subject up to 1903. It was not until 1911, however, that a mycologist was appointed, A. C. Tunstall taking up the post which he still holds. More recently H. Ashplant became Mycologist and Rubber Specialist to the United Planters' Association of Southern India.

India was the first of the tropical Dependencies to take up seriously the study of the parasitic fungi on, and the disease of, the crops grown by the people themselves, as distinct from the plantation crops grown under white supervision mainly for export. In the course of this work the necessity for gaining a knowledge of the fungous flora of the country became apparent and large collections were made by the Pusa staff and have been in great part worked out in collaboration with the Sydows of Berlin. Two earlier Indian mycologists had paved the way for this work. In a remarkable series of papers, published in the

Scientific Memoirs by Medical Officers of the Army of India and elsewhere from 1886 to 1892, A. Barclay contributed not only to a knowledge of the Uredinaceae of India but to the biology of this group as a whole. D. D. Cunningham, also an Indian Medical Officer, published between 1875 and 1897, a small but important series of memoirs on the genus *Choanephora* and on several other interesting fungi that cause plant diseases.

On the pathological side the staff at Pusa and in the Indian Provinces carried out studies on the diseases of cereals, pulses, root crops, oil seeds, drug and spice crops, fibres, palms and sugar-cane. The diseases of tropical fruits and forest trees have not yet been intensively studied either in India or in the other tropical Dependencies, while those of tea, rubber and coffee, the chief Indian plantation crops, have been dealt with mainly by the mycologists in private employ and by those of some of the native States, such as Mysore.

At the present time there are about a dozen mycologists, with a large number of assistants, at work in India, a number all too few for the requirements of the country.

In South Africa the first mycologist appointed was Illtyd Buller Pole Evans who, after a training under Marshall Ward, went as Mycologist to the Transvaal Government in 1905. When the Union was established he became chief of the Division of Plant Pathology and Mycology of the Union Department of Agriculture in 1911, and two years later chief of the Division of Botany and Plant Pathology. The establishment of this fine mycological centre is due to his unceasing pressure between 1907 and 1911 for a properly equipped central mycological laboratory at Pretoria.

In a country which was the birthplace of the father of mycology, Persoon, and where a succession of keen collectors from many nations had worked, it was fitting that Pole Evans should have commenced to study the indigenous fungi of South Africa at an early stage in his career, and should have been mainly instrumental in the formation of what is probably one of the best herbaria of fungi in any of the overseas parts of the Empire. A considerable part of his collections were worked out by the Sydows in Berlin, but the bulk are being dealt with locally. He was fortunate in his assistants and colleagues: Miss Ethel M. Doidge and Paul van der Bijl, who joined his staff shortly before the Union was established, and Miss Averil M. Bottomley, who was appointed in 1913, have all added extensively to the fungi known from South Africa. He himself paid particular attention to the rusts, in addition to a series of investigations on important plant diseases. As his administrative duties increased, Dr Doidge, who became assistant chief of the

Division, continued the more purely mycological work. Her monographic studies of the Ascomycetes, especially parasitic and epiphytic forms, are outstanding examples of the monographic treatment of peculiarly difficult groups. On the pathological side Dr Doidge has carried out a series of detailed studies of the bacterial diseases of plants in South Africa, having worked on some fifteen of these, of which four had previously been undescribed. Van der Bijl specialised in the study of the Polyporaceae of the country until he was appointed Mycologist in charge of the Natal Herbarium in 1917, when he took up the sugar-cane diseases that are of such vital importance to Natal, and worked also on various other phytopathological problems. On his transfer as Professor of Mycology in the University of Stellenbosch in 1921 he resumed his earlier interest in the Polyporaceae, of which he has published several lists, while more recently he has taken up the smuts. Two other mycologists have since joined the Division, more especially for the study of the diseases of cotton, tobacco and fruit.

In addition to the central Department, two of the Colonies in the Union have mycological officers. Victor A. Putterill was appointed Government Mycologist, Cape Colony, in 1920, after a period at Pretoria, and his work on fruit diseases is still being pursued in his recent post as chief Government Fruit Inspector at Cape Town. Van der Bijl was succeeded in Natal by H. H. Storey, whose work on the virus diseases of sugar-cane, maize and groundnut will be familiar to many pathologists. Counting the chiefs of the Division at Pretoria there are seven official mycologists in the Union, besides several university and agricultural college professors with mycological interests.

Rhodesia, which though not belonging to the Union may be considered here, has recently appointed a mycologist, J. C. Hopkins, after a considerable amount of collecting and some pathological work had been done by the Government Botanist, F. J. Eyles.

Canada was late in forming a purely mycological staff and has been influenced by developments in the United States in severely directing the work of the Government officers to the practical aspects of plant pathology, a science which in North America has become more and more divorced from mycology proper.

Little mycological work, even on the applied side, had been done when Hans T. Güssow, a native of Breslau who had been an assistant to William Carruthers, consulting botanist to the Royal Agricultural Society of England, was appointed chief of the newly established botanical branch of the Division of Experimental Farms in the Canadian Department of Agriculture

in 1909, with the title of Dominion Botanist. At first he had only a single assistant, and development was slow until the establishment of the field laboratories of plant pathology, of which there are now seven. The first of these was opened at St Catherines, Ontario, in 1912 and others followed in New Brunswick and Prince Edward Island in 1915, in Manitoba and Saskatchewan in 1917, in British Columbia in 1921, and in Nova Scotia and Quebec more recently. That in Manitoba has been absorbed into the newly established Dominion Rust Research Laboratory at Winnipeg, a very fine and up-to-date institution where there is a staff of seven pathologists engaged in the study of cereal diseases under the leadership of D. L. Bailey. At the Central Experimental Farm in Ottawa, the Dominion Botanist has a staff of five pathologists, some of whom are in charge of special branches such as forest pathology, bacterial diseases, and general mycology and plant disease survey.

Besides these officers of the Dominion Department, two of the Provinces, namely British Columbia and Manitoba, have each a Provincial Plant Pathologist, and the Canadian Forest Products Laboratory at Montreal has two pathologists for the study of timber decay. There are altogether more than thirty official plant pathologists employed in the investigation of the cause and control of plant diseases in Canada at the present time.

It is impossible to give an adequate survey in a short space of the field of work covered by such a large number. Güssow himself made valuable contributions to the science of plant pathology in several scientific papers and in the bulletins and annual reports of the Department over a period of years. J. W. Eastham, who was the first scientific assistant on the Dominion Botanist's staff that specialised in plant diseases and who is now Provincial Plant Pathologist in British Columbia, has worked chiefly on fruit diseases, as did Rankin, Hockey, Berkeley and others; Fraser, Bailey and Miss Newton have greatly contributed to knowledge of the biology and control of Canadian cereal diseases; Murphy and Bisby have worked on potato diseases; McCallum on tree diseases.

In the study of the fungous flora of Canada it cannot be said that the official plant pathologists have played a great part. Fraser and Connors have monographed the rusts of the Prairie Provinces and Bisby has published a list of Manitoba fungi in collaboration with Professor Buller.

Even amongst the non-official workers in the Universities and elsewhere systematic mycology has been largely neglected. Faull and Bell have made systematic studies of some forest tree rusts, but the former is better known from his pathological and cytological work and most of the other academic workers have

confined their mycological interests to the fungi as producers of disease. Probably the largest contribution to knowledge of the Canadian fungi has been made by an amateur, Dr John Dearness, whose collections and descriptions are well known to all students of North American fungi.

As a contributor to knowledge of the biology of the fungi in its widest and most varied aspects Arthur H. R. Buller, Professor of Botany in the University of Manitoba, stands alone. Going out from the University of Birmingham in 1904, he published the first volume of his *Researches on Fungi* in 1909 and in the subsequent volumes of this work and in many single papers he has not ceased to elucidate the inner secrets of the life of these plants. Both in time and in the importance of his contribution, his rank amongst the pioneers of mycological development in the British Empire overseas is secure.

In British tropical Africa the first official mycologist was Charles Ogilvie Farquharson who, after training at Aberdeen and work in the Jodrell Laboratory, Kew, went out as Mycologist in the Agricultural Department of Southern Nigeria in 1911. His tragic death by drowning at sea, when homeward bound during the last few weeks of the war, cut short a career of unusual promise. Walter John Dowson took up the position of Mycologist in the Department of Agriculture, British East Africa (now Kenya) in April, 1913. A month earlier William Small started work in the neighbouring colony of Uganda as Government Botanist and at once concentrated his attention on the diseases of plants to which he continued to give most of his time until he became officially the Mycologist to the Department of Agriculture in 1920. In the Gold Coast, Robert Hugh Bunting was appointed Government Mycologist in 1915, in addition to being Assistant Director of the Department of Agriculture. These were the four pioneers of the development of economic mycology in tropical Africa. Further appointments were made in rapid succession after the war, until at present there are two mycologists in the Gold Coast, two in Nigeria, and one each in Kenya, Uganda, Tanganyika, and Sierra Leone. Zanzibar also employed one for special work on clove diseases during a period of six or seven years.

The work in each of these Colonies has been naturally determined mainly by the nature of the local agriculture. In Kenya, Dowson and his successor, McDonald, have done much in the study of the diseases of the coffee bush; in the Gold Coast, Bunting and Dade have concentrated chiefly on cacao diseases; and in Uganda, with its more diverse agricultural interests, Small worked on diseases of coffee, cereals, and various native crops. In all parts of British tropical Africa plant diseases are

being intensively studied at present, but it will be many years before they are adequately known and the full extent of their depredations realised. The first general handbook of plant diseases in any part of this vast area that has appeared is Bunting and Dade's *Gold Coast Plant Diseases* published in 1924. Apart from the parasites, relatively little attention has been given to the fungous flora, though Farquharson and MacFie in Nigeria, Bunting in the Gold Coast, Dummer, Maitland, and Small in Uganda, and Maitland and Dowson in Kenya have made considerable collections, some of which have been worked out at Kew. There is no doubt that our relative ignorance of the fungi of tropical Africa is a serious handicap to economic mycological work in that part of the Empire.

Though no longer a part of the Empire, Egypt deserves mention here, if only on account of the pioneering work on cotton diseases carried out by W. Lawrence Balls between 1904 and 1913, when he was botanist to the Khedivial Agricultural Society and the Department of Agriculture. A whole time mycologist, however, was not appointed until after the war, when H. R. Briton-Jones was given the post.

A combined post of Botanist and Mycologist was created in the Mauritius Department of Agriculture in 1922 when E. F. S. Shepherd from Macdonald College, Quebec, was appointed to it. Even in the far Pacific, a Government Mycologist, J. G. C. Campbell, is at work in the Fiji Islands.

In the Dominions, Colonies and Protectorates there are now about a hundred mycologists and plant pathologists in Government Service, counting only those whose duties include some form of research or experimental work. As I have shown, this development has come about almost entirely since the beginning of the present century. It has resulted from the tremendous development that has taken place during the same time in the demand for the agricultural produce of these countries. All these staffs are engaged in the study or control of plant diseases. The value of the crops whose health they have to safeguard is enormous. The agricultural exports of the Colonies alone, excluding the Dominions and India, were worth £171,000,000 in 1926. Rubber was exported, chiefly from Malaya and Ceylon, to a value of not far short of £100,000,000. In tea, rubber and coconut produce Ceylon exported over £33,000,000 worth in 1925. In the same year India exported over £20,000,000 worth of tea, about £65,000,000 worth of raw and manufactured jute and over £60,000,000 worth of raw cotton, all grown in the country. Of crops mainly used in the country there are

80,000,000 acres under rice in India, and 30,000,000 (yielding 10,000,000 tons) under wheat. The Gold Coast supplies more than half the world's requirements of cocoa, exporting £8,000,000 to £10,000,000 worth annually.

Figures like these mean little, however, unless it is remembered that the agricultural industry is almost the only one in many of the Colonies. Their whole prosperity is bound up with it and they are threatened with ruin when an epidemic disease breaks out in one of their main crops. The disasters that overtook Ceylon when its coffee industry was destroyed by leaf disease, and the West Indies when rind disease of sugar-cane swept the old varieties of cane out of existence, may be repeated at any time and indeed have been repeated on a smaller scale quite recently, when withertip of limes destroyed 90 per cent. of the crop on some estates in Dominica in a year or two after its first appearance and forced the island to appeal to the home Government for relief. That such outbreaks are not more frequent can be attributed in great measure, I think, to the work of the economic mycologists. No one can doubt, who knows the facts, that the rubber industry of Malaya has been saved not once but several times by the control measures devised by the local mycologists against such diseases as pink disease and mouldy rot, and if the present uneasiness about the spread of the rubber *Oidium* becomes justified, as it well may, a greater effort than any in the past will be required to protect this enormous industry.

It is difficult for people in this country to realise why disease becomes so much more dangerous a factor in the agriculture of these newly developing countries than it is at home. The first great difference between the conditions in the two cases is the tendency to plant large areas continuously or almost so under the same crop. This is true not only in permanent plantation crops proper, like tea and rubber, where one may pass for miles on end through the crop, broken only occasionally by a belt of jungle, but it is even more true for the cereal areas of Canada and Australia. Parasites find optimum conditions for their depredations under such circumstances. A spore liberated from an infected plant stands a good chance of landing on a susceptible host, and every individual plant undergoes such an intensive bombardment that the weak spots in its defences are likely to be attained. Then, a low cost of production is essential if the produce has to be sent long distances to its market, and it is not possible to pay the same attention to the general sanitation of the plants as is given under more intensive agricultural conditions. And, finally, the crops are often relatively new introductions and there has been as yet no time for the

action of the process of selection of disease-resistant varieties that has consciously or unconsciously been going on in the older countries for generations. The economic mycologist overseas is thus continually liable to be faced with outbreaks of disease of a much more severe type than are usually encountered at home, and that can only be paralleled by attacks of newly introduced diseases, such as American gooseberry mildew or wart disease of potatoes, in Britain. He is fortunate, indeed, when he has to deal with a known parasite with the means of control already worked out.

On the human side, too, the work is of not less absorbing interest. One must have experienced it, to know what it means to find a native village that has specialised in the growth of some particular crop or variety faced with the total loss of that crop by an unknown disease. When large districts are similarly affected the matter soon comes to light, but small areas may suffer in silence. When one can help these people one is fortunate, but failure owing to the obscurity of the disease or want of time for working it out is still too frequent. An equally painful impression is left when the white planter who has, perhaps, put all he possesses into a tea or coffee plantation in one of the colonies finds fifty or seventy-five per cent. of his bushes suffering from a disease on which not enough work has yet been done to allow of adequate control measures being recommended. Such cases make the observer feel that no increase in the numbers of men engaged in the struggle against plant disease in these mainly agricultural countries can be too rapid; that a constant supply of new men trained in their study is wanted; and that there is no field of mycology which better repays cultivation than that worked by the mycological and plant pathological departments in the overseas parts of the British Empire.

STRAINS AND TAXONOMY OF PHYTOPHTHORA PALMIVORA BUTLER (P. FABERI MAUBL.).

By S. F. Ashby, Mycologist, Imperial Bureau of Mycology.

(With nine Text-figures.)

Observations by economic mycologists during the last ten years especially, have shown that the omnivorous tropical species under consideration exists as a number of morphologically distinguishable and in some instances biologically distinguishable strains on a wide range of cultivated plants. It has been recognised as causing a fruit rot and patch canker of cacao (1) in

most countries where that crop is cultivated; a fruit and shoot rot, leaf fall and patch canker of *Hevea* rubber in Ceylon (1); patch canker and black stripe disease of *Hevea* rubber in Java (2) (it has been isolated from black stripe disease of *Hevea* rubber in Malaya); fruit rot and stem rot of papaw (*Carica papaya*) and fruit rot of breadfruit (*Artocarpus incisa*) in Ceylon (1); patch canker of nutmeg in Java (2); fruit rot of cotton in the West Indies (3); fruit rot of *Mimusops* sp. in the Gold Coast; shoot rot of *Citrus* spp. in the Philippines (4); bud rot of palms in India, Ceylon, the Philippines and the West Indies (5); and rots of orchids, etc. in Ceylon (1) and Java (6).

Isolations from cacao and the coconut have been studied in pure culture by a number of observers in both West and East Indies. Gadd (1) in particular made a careful comparative study of seven isolations from six host plants in Ceylon and showed that all could be referred to the same species. He observed that the isolations from cacao and papaw formed, on culture media, sporangia which were relatively broader, and chlamydospores which were larger than the isolations from *Hevea* rubber, breadfruit, *Dendrobium* and *Odontadenia*, and was therefore able to place them in two morphological groups which, for convenience, he called the "cacao" and "rubber" groups respectively. The arrangement was also found to correspond with a biological grouping, as oospores were developed only when a member of one group was grown with a member of the other group.

With a view to determining if these observations were applicable to isolations made elsewhere from the same or other hosts and also in the hope of ascertaining the limits of the species more definitely, I collected as many isolations in pure culture as could be obtained and grew them on such standard media as bean-meal, quaker oats and maize-meal agars*. They were inoculated in the middle of slopes of the freshly prepared media, grown for a week at 23° C. and then at the temperature of the laboratory.

It was found that the cultures could be separated into a group of strains which was taken as typical of the species, and a group of atypical strains. A typical strain spread rapidly over the surface of the agar for the first two to three days and then developed an increasing, moderate white aerial mycelium during the following week or more; characteristic was the formation of

* These were prepared by grinding to powder mature, dry, white french beans, dry quaker oats or whole grains of maize in a coffee mill, heating four to six parts with one hundred parts of water in a glazed beaker in a boiling water bath for about twenty minutes, adding 1·2–1·5 per cent. of "bacto" agar, boiling for a further ten minutes, pouring through cheese-cloth which was squeezed, and autoclaving in $\frac{3}{4}$″ by 6–7″ tubes. To obtain good growth the medium was made fairly thick and contained a good deal of suspended matter

sporangia after two to three days which became very abundant during the succeeding three to four days, so that the upper part of the slope acquired a mealy appearance. Examination showed that the sporangia were terminal in sympodia of a half dozen or more on simple or branched sporangiophores. When a bent platinum needle was swept over the aerial growth on the upper part of the slope after five to seven days and then touched to a drop of water, mature sporangia separated readily and abundantly from the sporangiophores. The sporangia were typically oval (lemon-shaped) with a well-marked papilla occupied by a hyaline plug of appreciable depth, and each bearing a short, more or less occluded, often stout pedicel, mostly 2–4 μ long and not exceeding 6 μ in length; a thickening was frequently present in the base of the cavity of the sporangium above the attachment of the pedicel. The short stalk, so constantly present, was due to natural abscission at the point where the branch bearing the succeeding sporangium in the sympodium arose; in some strains the sporangiophore tended to be enlarged at the point of origin of such branches. When the mature sporangia from cultures five to seven days old were brought into cool, well-aerated water, a number showed segmentation of the granular contents and discharged zoospores within fifteen to thirty minutes. Bean-meal agar (french or lima beans) was found to be the best medium for producing a high proportion of functional zoosporangia. On the oat, and to a less extent on the maize media, a relatively small proportion of the sporangia were functional even in cultures a week or less old, and on all media the proportion lessened as the age of the cultures increased. The number of zoospores produced by each sporangium depended upon its size and varied from ten to over forty. In addition to sporangia, another asexual spore began to develop contemporaneously and became abundant during the second week of growth and subsequently; it was a spherical or subspherical, smooth-walled, unicellular body which was borne either terminally or subterminally on the hyphae or on shortened and sometimes inflated branches, or finally intercalated in the hyphae, but never in sympodia; like the sporangia these bodies were borne on the aerial, the surface, and the immersed mycelium; the contents were granular with or without a large vacuole, and the wall thin or thick, hyaline or yellowish-brown; in old cultures, especially in those grown at high temperatures, the walls were often thickened and coloured, and the contents finely granular, small vacuoles in contact with the walls giving an appearance of germ-pores; these bodies were incorrectly described in the earlier literature as oospores but their asexual nature was recognised in the later literature under the terms

resting-conidia or, more frequently, chlamydospores. They germinated by one or more germ-tubes and did not appear to require a period of rest before doing so; germination in water was often scanty, and when it occurred, the short germ-tubes usually terminated in single sporangia or reduced sympodia. These bodies differed from the terminally borne sporangia in not separating by natural abscission from the hyphae. Oat media appeared especially to favour production of chlamydospores. In all cultures a small proportion of sporangia were borne intercalated in the hyphae; they were subspherical or more broadly oval than the terminal sporangia and differed in appearance from chlamydospores only in having a papilla. Sporangia, either terminal or intercalated, which fail to function as zoosporangia, germinate directly like chlamydospores, and they frequently do so in cultures by means of a germ-tube arising just below and to one side of the papilla and terminating in a sporangium; a succession of sporangia produced one from another in this way may be found in old cultures each being smaller than its predecessor.

Typical strains characterised by early and abundant production of sporangia were those isolated by the author (3, 7) from the coconut in Jamaica; from cacao in Trinidad, Grenada and Jamaica and from cotton in St Vincent (3); by H. A. Dade from cacao and *Mimusops* sp. in Gold Coast; by Gadd (1) from *Hevea* rubber in Ceylon; by Ocfemia and Roldan (4) from citrus in the Philippines; by Sundararaman from the coconut in India; and by A. Thompson from black-stripe disease of *Hevea* rubber in Malaya. Cultures considered atypical, on the other hand, were characterised by a marked reduction in, or almost complete suppression of the production of sporangia; aerial mycelium was frequently more abundant than in typical cultures and chlamydospores were always freely and rapidly developed, especially on the oat and maize media. In some instances, where sporangia were very scanty, chlamydospores were especially abundant. When young mycelium of both typical and atypical cultures was transferred to water, sporangia were developed freely in sympodia after two to three days at temperatures of 20–25° C.

Most of the atypical cultures examined were obtained from "culture collections" where they had been maintained for some years; they included isolations by Reinking (8) from the coconut and cacao in the Philippines; by Gadd (1) from cacao, breadfruit and *Dendrobium* in Ceylon; by Miss Schwarz (6) from *Vanda* sp. and *Cattleya* sp. in Java; by Tucker (9, 10) from coconut and Sabal palm (received direct) in Porto Rico and by Stahel from cacao in Surinam. The descriptions of most of these cultures, when freshly isolated, indicated that sporangia were developed

freely on the solid media, that in fact they were typical, so that it would seem that subsequent maintenance on poor substrata, probably at low temperatures, resulted in partial or almost complete suppression of sporangial production; transfers to richer media and growth at a favourable temperature did not restore the original habit. My isolation from the coconut in Jamaica has been in continuous culture for seven years in the tropics and two years in a temperate climate—nine years in all, during which period it had been transferred between thirty and forty times; its typical character has been retained and the sporangia have undergone no appreciable change in size and shape; it has, however, been maintained on lima bean, french bean and quaker oats agars of good consistency so that growth was always vigorous, and care has been taken to keep the cultures free from bacterial contamination. Similarly, the isolations made six years ago from cotton in St Vincent and three years ago from cacao in Trinidad have also retained the original characters unchanged. The cultures of the coconut and cacao isolations which had been out of my hands for three years were found recently to be atypical; the sporangia had also changed in shape, having become relatively broader. Some isolations appear, however, to have been atypical in culture from the outset as Gadd (I) has recorded for those from *Odontadenia* and papaw.

Following Rosenbaum (II), several authors, notably Gadd, have used biometrical methods in an attempt to record with precision the size and shape of the sporangia and size of the chlamydospores in the various isolations. Both of these asexual reproductive bodies, the sporangia especially, are, however, very sensitive to external conditions, humidity, nature of substratum and age of culture all affecting size and shape appreciably, so that precise figures are of little significance; nevertheless, these organs in a number of isolations when grown under comparable conditions on the standard media, retain characteristic relative differences in shape (sporangia) or size (chlamydospores), so that some degree of morphological stability can be recognised. The isolations from *Hevea* rubber in Ceylon and from the coconut in the West Indies for instance, have always hitherto developed sporangia which are narrower and chlamydospores which are smaller than the cacao strain of Ceylon, West Indies and West Africa, when they are grown in parallel culture. Table I shows the effect of age of culture upon the size and shape of the sporangia of the West Indian coconut strain. In Table II the influence of scanty nutrition or lack of nutrients is indicated for the West Indian cacao and coconut strains. Table III is a compilation of the recorded mean size and range of the sporangia

for a number of isolations from various hosts in the American, African and Asiatic tropics; the figures are based on measurements of a minimum of a hundred sporangia (in most instances several hundred); the figures for the West Indian and West African cacao strain and the Jamaica coconut strain cover, for each strain measurements of a total of about two thousand sporangia from a number of isolations on different standard media, the variations in the mean size and mean ratio (relation of length to breadth) being also recorded. In Table IV are similar records for the chlamydospores. Further references to some of these data will be made later.

Until 1922 it was believed that sexual organs were not produced by this species, the records of oospores by the earlier authors notably Butler (12), Von Faber (13), Coleman (14) and Rorer (15) either on or in the host tissues* or in culture, having reference to the so-called resting conidia or chlamydospores which, however, are produced also by related species such as *P. parasitica* and *P. Colocasiae* in addition to true oospores. In that year I recorded (3) the occurrence of oospores in mixed cultures of the West Indian cacao strain with the Jamaica

Table I. Phytophthora palmivora. *Influence of the age of the culture on the size and shape of sporangia of the Jamaica coconut strain.*

Age (days)	Substratum	Temp. ° C.	Number measured	Mean size	Ratio	Range
6	Lima bean agar	20–30	100	54 × 31	1·75	36–66 × 25–37
12	Do.	20–30	100	50·2 × 31·3	1·60	40–64 × 27–36
21	Do.	20–30	100	43·0 × 28·3	1·51	29–51 × 19–35

Table II. P. palmivora. *Influence of diminished nutrition or lack of nutrients on the size and shape of sporangia.*

Strain	Sub-stratum	Temp. ° C.	Age (days)	Mean size	Ratio	Range
Cacao (W. Indies)	Bean agar film in damp cell	25	6	38·7 × 24·4	1·60	—
Do.	Do.	25	11	36·0 × 23·3	1·55	—
Do.	Water	23	2–3	(1) 39·8 × 26·8	1·48	24–51 × 20–34
				(2) 37·8 × 26·2	1·44	27–51 × 20–34
Do.	Cacao pod	20–30	1	39·0 × 24·3	1·60	29–50 × 19–30
Coconut (Jamaica)	Bean agar film in damp cell	25	3	44·0 × 25·2	1·75	—
Do.	Do.	25	6	41·0 × 25·3	1·62	—
Do.	Do.	25	12	40·0 × 25·0	1·60	—

* In 1920 (7) I recorded the occurrence of oospores with amphigynous antheridia in a spot on the base of a leaf of a coconut tree in Jamaica infected by this *Phytophthora*. The mean size of twenty-one oospores was 26 μ and the range 24–29 μ.

Table III. P. palmivora. *Measurements of sporangia in microns.*

Host	Country	Observer	Substratum	Age of culture	Mean size	Mean ratio	Range
Cacao	Jamaica, Trinidad, Grenada, Gold Coast	Author	Bean-meal, quaker oats and maize-meal agars	5–11 days	49·0 × 30·6	1·60	36–62 × 24–36
Do.	Jamaica	Do.	Cacao pod—damp chamber	1 day	37·7 × 22·3	1·68	29–47 × 19–27
			Cacao pod—dry air	Do.	39·5 × 24·9	1·59	31–50 × 23–30
Coconut	Do.	Do.	Bean-meal, quaker oats and maize-meal agars	5–11 days	53·5 × 31·0 (48–62 × 29–33)	1·73 (1·60–1·90)	36–66 × 24–37
Do.	Do.	Do.	Fruits and leaf stalks	—	48 × 29 (45–51 × 28–29)	1·66 (1·56–1·76)	33–72 × 22–40
Do.	Porto Rico	Tucker	Maize-meal	8–10 days	52·7 × 31·0	1·70	26–88 × 18–41
Do.	Philippines	Reinking	Oatmeal agar	9–11 days	52·3 × 31·3	1·68	20–83 × 14–45
Do.	India	Author	Bean-meal and quaker oats agars	6–13 days	54·0 × 35·0	1·54	39–76 × 25–46
Palmyra and coconut	Do.	Butler	Leaf sheaths and pinnae	—	50 × 35	1·43	38–70 × 33–42
Cacao	Trinidad	Rosenbaum	Oat agar	A few days	48·5 × 32·3	1·50	34–66 × 20–48
Do.	Ceylon	Gadd	Maize-meal agar	5 days inoculated with a pure culture	48·2 × 34·1	1·42	—
Do.	Do.	Do.	Cacao pod		45·5 × 27·6	1·65	—
Do.	Do.	Do.	Rubber fruit		42·1 × 25·5	1·65	—
Hevea rubber	Do.	Do.	Maize-meal agar	5 days inoculated with a pure culture	47·9 × 26·5	1·79	—
Do.	Do.	Do.	Rubber fruit (*a*)		39·6 × 24·0	1·65	—
Do.	Do.	Do.	Do. (*b*)		47·4 × 27·1	1·76	—
Do.	Do.	Do.	Do. (*c*)		44·2 × 27·3	1·62	—
Hevea rubber (Gadd's strain)	Do.	Author	Bean-meal agar	8 days at 23° C.	45·1 × 26·4	1·71	31–62 × 22–39
Do.	Do.	Do.	Quaker oats agar	Do.	47·0 × 27·0	1·74	37–66 × 22–36
Papaw (*Carica papaya*)	Do.	Gadd	Maize-meal agar	5 days	(*a*) 49·8 × 32·6	1·55	—
Breadfruit (*Artocarpus incisa*)	Do.	Do.	Do.	Do.	(*b*) 48·4 × 32·4	1·56	—
Citrus spp.	Philippines	Ocfemia	Oatmeal agar	2–4 weeks	49·6 × 27·4	1·80	—
Do.	Do.	Author	Bean-meal and quaker oats agars	9 days	44·7 × 29·5	1·52	25–65 × 18–39
Hevea rubber (black-stripe disease)	Malaya	Do.	Bean-meal agar	6 days	49·2 × 34·0	1·45	37–58 × 26–42
Mimusops sp.	Gold Coast	Do.	Quaker oats agar	6 days	50·2 × 30·2	1·66	—
Sea-island cotton	St Vincent	Do.	(*a*) Bean-meal agar	6 days	43·3 × 29·5	1·47	—
			(*b*) Quaker oats agar	Do.	61·6 × 30·3	2·03	—
					56·8 × 28·2	2·0	—

Table IV. P. palmivora. *Measurements of chlamydospores in microns.*

Host	Country	Observer	Substratum	Mean size	Range
Cacao	Jamaica	Author	Bean-meal agar	38·0	21–49
Do.	Trinidad	Rosenbaum	Oat agar	39·0	28–59
Do.	Ceylon	Gadd	Maize-meal agar	39·6	25–57
Do.	Do.	Do.	Cacao pod	37·0	—
Do.	Philippines	Reinking	Oatmeal agar	41·0	18–53
Coconut	Jamaica	Author	Bean-meal and quaker oats agars	36·1	19–49
Do.	Do.	Do.	Leaf stalks and pinnae	31·0	19–52
Do.	Porto Rico	Tucker	Maize-meal and potato dextrose agar	34·8	19–49
Sabal palm	Do.	Do.	Leaf stalk	32·6	—
Coconut	Philippines	Reinking	Oatmeal agar	41·6	19–61
Do.	India	Author	Bean-meal and quaker oats agars	39·1	24–58
Palmyra and coconut	Do.	Butler	Leaf stalks and pinnae	Between 35·0 and 45·0	25–45
Papaw (*Carica Papaya*)	Ceylon	Gadd	Maize-meal agar	38·8	28–50
Hevea rubber	Do.	Do.	Do.	35·5	22–48
Do.	Do.	Do.	Cacao pod	37·9	—
Breadfruit	Do.	Do.	Maize-meal agar	35·4	—
Citrus sp.	Philippines	Ocfemia	Oatmeal agar	33·5	19–49

coconut strain and also with an isolation from cotton in St Vincent; when the latter two were grown together oospores were not produced. Although the three isolations were morphologically similar, though not identical, it was thought that two species were concerned, but this view was later given up and they were recognised as strains of the same species (16). Gadd (1) confirmed this observation by obtaining similar oospores when some of his isolations in Ceylon were grown together in pairs: some pairs, however, failed to produce them. He found, as mentioned already, that this biological behaviour paralleled some minor morphological differences in the asexual spores so that the strains fell into two groups—the "cacao" and "rubber" groups. To determine if this behaviour was of more general occurrence I grew a considerable number of strains together in pairs, using as medium the maize-meal agar which Gadd employed. The inocula were planted about an inch apart on the sloped medium in tubes, maintained for a week at a temperature of about 23° C. and then transferred to the cooler, variable room temperature. The strains which it was desired to test were grown at first with the Trinidad cacao strain and the Jamaica coconut strain and later with other strains representing the two groups. The mixed cultures were kept under observation for from three to six months. The outcome was definite and concordant—

oospores were either produced promptly and abundantly or were not formed even after several months. In all the mixtures in which sexual organs occurred they were present four to five days after the cultures were set up and fully developed oospores could be found after five to six days in the zone intervening between the inocula. The reaction when it occurred was prompt and definite with both typical and atypical cultures. At tropical temperature the development of oospores had been comparatively slow—one or two months being required before they were present in appropriate paired cultures in appreciable numbers, the delay in their development being due probably to the high day temperature (usually near 30° C. for several hours). The sexual organs in all mixtures showed only amphigynous antheridia. Adopting Gadd's group nomenclature the arrangement of the strains was the undermentioned:

"Cacao" group.

Host	Country	By whom isolated	Source of culture
Cacao	Trinidad	Author	—
Do.	Surinam	Stahel	C.S.
Do.	Gold Coast	Dade	H. A. Dade
Do.	Ceylon	Gadd	C.S. and L.I.
Do.	Trinidad	Author	A.T.C., No. 1413 (*P. Faberi*)
Coconut	India	Sundararaman	A. Thompson
Papaw	Ceylon	Gadd	L.I.
Vanda sp.	Java	Schwarz	C.S.
Cattleya sp.	Do.	Do.	Do.

"Rubber" group.

Coconut	Jamaica	Author	—
Do.	Porto Rico	Tucker	C. M. Tucker
Do.	Philippines	Reinking	C.S.
Sabal Palm	Porto Rico	Tucker	C. M. Tucker
Mimusops sp.	Gold Coast	Dade	H. A. Dade
Citrus	Philippines	Ocfemia and Roldan	G. O. Ocfemia
Hevea (black stripe)	Malaya	Thompson	A. Thompson
Cacao	Philippines	Reinking	L.I.
Breadfruit	Ceylon	Gadd	Do.
Hevea rubber	Do.	Do.	Do.
Dendrobium sp.	Do.	Do.	Do.
Odontadenia sp.	Do.	Do.	Do.
Coconut	Jamaica	Author	A.T.C., No. 1418 (*P. palmivora*)
Do.	Do.	Do.	C.S. (*P. palmivora*)

C.S. = Centraalbureau voor Schimmelcultures, Baarn, Holland.
L.I. = National Collection of Type Cultures, Lister Institute.
A.T.C. = American Type Culture Collection, Chicago.

The sexual organs began to develop first in the zone of contact of the two vegetations but could be found later, abundantly

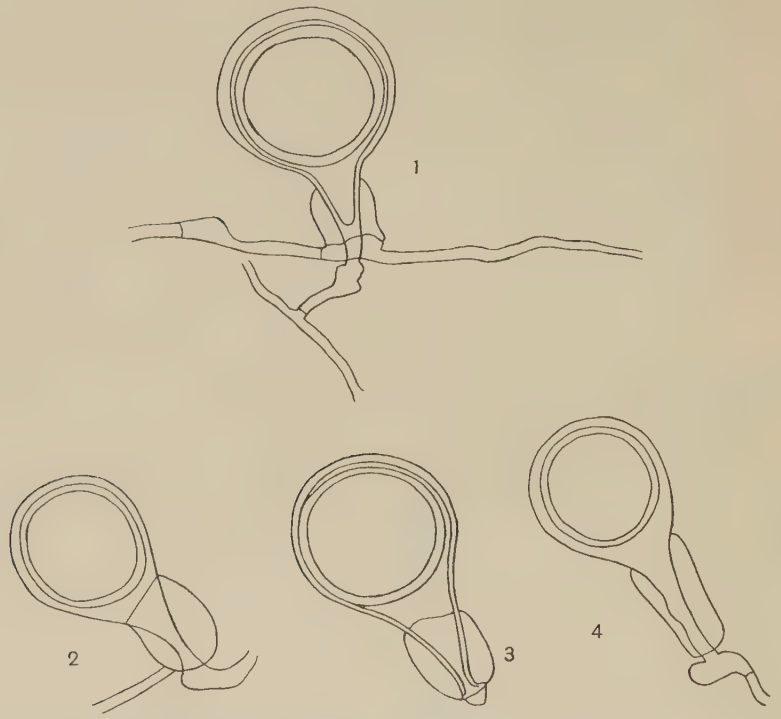
throughout both vegetations, or in some instances in quantity only in the growth zone of the upper inoculum, being either scanty, absent or restricted to the upper part of the lower vegetation. Measurements of the oospores in the growth zone of each inoculum in a number of the paired cultures are recorded in Table V. It may be observed that the mean size and range

Table V. P. palmivora. *Measurement of the oospores of some strains grown in pairs on maize-meal agar.*

Pair	Age of culture	Growth zone	Oospores: Number measured	Oospores: Mean size	Oospores: Greatest frequency or "mode"	Oospores: Range
1. *Mimusops*—upper						
Cacao	3 weeks	*Mimusops*	50	24·1	23·9	18·8–29·0
(Trinidad)—lower	2 months	Do.	50	29·6	31·0	22·0–41·6
	9 months	Do.	37	(*a*) 25·0	23·9	20·0–29·0
	Do.	Do.	54	(*b*) 31·8	31·0	24·0–41·0
			91 (*a*) and (*b*)	29·2	31·0	20·0–41·0
	5 months	Cacao	50	23·6	23·9	19·0–29·0
2. Coconut						
(India)—upper	2 months	Coconut (India)	50	31·5	31·5	27·0–41·0
Coconut						
(Jamaica)—lower	Do.	Coconut (Jamaica)	50	26·8	26·4	22·0–31·5
	9 months	Do.	50	26·7	26·4	23·0–31·0
3. Coconut						
(India)—upper	2 months	Coconut (India)	50	31·8	30·6	26·0–39·0
Cotton						
(St Vincent)—lower	Do.	Cotton	50	27·3	27·2	22·0–32·5
4. *Hevea*						
(Malaya)—upper	2 months	*Hevea*	50	27·6	27·2	22·0–33·0
Cacao						
(Trinidad)—lower	Do.	Cacao	50	25·0	{23·8 {26·4	20·0–30·0
5. *Citrus*						
(Philippines)—upper	2 months	Citrus	50	24·3	23·9	19·5–29·0
Coconut						
(India)—lower	Do.	Coconut	None found	—	—	—

of the oospores differed materially after two months in the two growth zones in some cultures. My earlier observations and those of Gadd (1) and Lester-Smith (17), indicated a mean size for the oospores between 23 and 24 μ with a range of 17–29 μ; these dimensions apply also in three instances recorded in Table V—namely, to the *Mimusops* zone after three weeks, the cacao zone after five months, and the zone of the citrus strain after two months. The changes in the size and appearance of the sexual organs in the *Mimusops* zone have been recorded and may apply also to those in the growth zones of the coconut and cotton strains. After three weeks the *Mimusops* growth zone showed

sexual organs having yellowish-brown, thick-walled, broadly funnel-shaped oogonia (Figs. 1–3), the exclusively amphigynous antheridia frequently enveloping only the lower ends of the oogonial stalks. After two months a second batch of sexual organs had developed in the same zone, characterised by thin-walled, hyaline oogonia of a less pronounced funnel-shape and



Figs. 1–4. Oospores and broadly funnel-shaped oogonia in the vegetation of the *Mimusops* strain in a paired culture with the cacao strain (Trinidad) on maize-meal agar. × 750.

larger oospores filled with a single oil globule. The measurements made at two months covered both the early and late crops of oospores, the "mode" being that of the more numerous later crop. After nine months (autumn and winter room temperature) there was no change in the mean size, mode and range; the early crop of oospores (*a*) was easily distinguished by the yellow thickened oogonial walls from the later crop, (*b*) with the hyaline, thin-walled oogonia so that both could be measured separately; the later-formed, larger oospores being the more abundant, determined the "mode." In the zone of the cacao strain in the same tube, the sexual organs showed only yellow, thickened

oogonial walls with a short, narrow stalk so that the spherical part of the oogonium appeared to rest directly on the antheridium (Fig. 5); in this zone the oospores showed the dimensions previously recorded by Gadd and myself. In culture No. 4 the measurements of the oospores in the growth-zone of the cacao strain showed two modes, one similar to that which is characteristic of oospores in the growth-zone of that strain, and the other similar to that of the oospores in the zone of the *Hevea* strain. The oogonia in the growth zone of the Indian coconut strain resembled those of the *Mimusops* strain, being mostly long and broadly funnel-shaped; on the other hand, the oogonia in the growth-zones of the West Indian and Philippine coconut strains, and the cotton and most of the other strains, resembled those of the cacao strain. The data appear to indicate that the oospores of some strains of the species may differ appreciably in size from those of others, recalling similar differences in strains of *P. parasitica* (18).

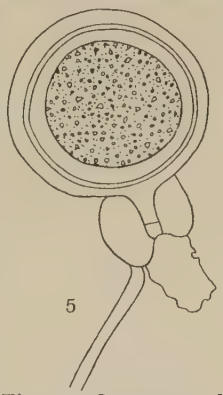


Fig. 5. Oospore and characteristic spherical oogonium with a slender stalk in the vegetation of the cacao strain in the same culture as Figs. 1–4. × 750.

To explain the behaviour of the strains in paired culture Gadd (1, 5) supposes that the mycelia are unisexual, the members of the "cacao" group being potentially female and those of the "rubber" group, male, the sexual organs being developed in consequence of a stimulus imparted to the one vegetation by the other (male). I recorded, however (3), the development of oospores of size and range similar to those in paired cultures of *P. palmivora* when the cacao strain was grown with a strain of *P. parasitica* (microspora) the mycelium of which is bisexual. Lester-Smith (17) has followed up this observation and obtained similar oospores in cultures of both the cacao strain and the West Indian coconut and cotton strains, and therefore in the members of both groups, when paired with each of three isolations of *P. parasitica* (microspora); these oospores Gadd considers to be hybrid. Lester-Smith, on the other hand, maintains the view that all strains of *P. palmivora* are potentially bisexual and might therefore be expected to form oospores in pure culture under, as yet unknown, conditions. In accordance with the latter view, when strains of the two groups of *P. palmivora* are paired, the development of oospores after a few days is due to a biochemical stimulation of the one vegetation by the other, resulting in the development of both antheridia and oogonia on each mycelium or dominantly on one of them; this view does not exclude crossing but subordinates it to autogamy. Observed

differences in the size of the oospores and form of the oogonia under the two vegetations in the same culture appear to lend support to this view.

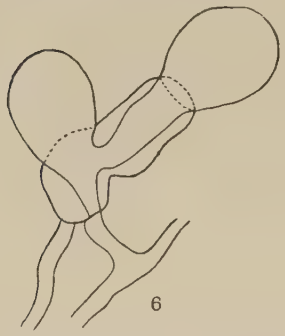


Fig. 6. Branched antheridia with oogonia, from the same culture; the sexual organs were void of contents and had apparently ceased to develop. × 750.

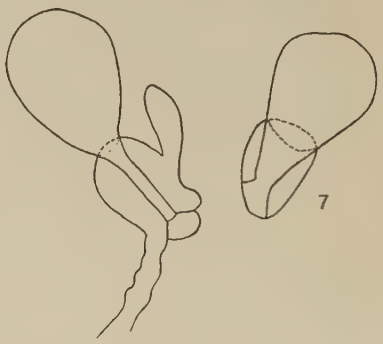
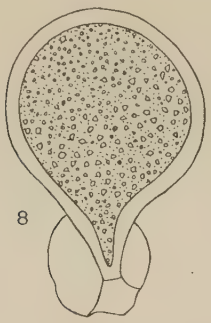
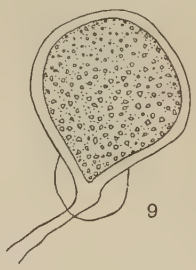


Fig. 7. Simple antheridia and oogonia arrested in development; from the same culture. × 750.





Figs. 8 and 9. Thick-walled oogonia with persistent antheridia; the oogonia resemble chlamydospores strongly (3). × 750.

If the pairs belong to the same group the mycelia are indifferent and no stimulus is imparted. A check to growth of a general kind, such as Murphy (19) supposed to be the cause of the prompt development of oospores in the zone of contact of two colonies of *P. erythroseptica* which has a bisexual mycelium, cannot explain the presence and absence of oospores in paired cultures of *P. palmivora*. When strains of that species are grown with the same strain of *P. parasitica*, the development of oospores in the growth zone of the first is more delayed; it does not appear that the *parasitica* strain exercises any direct stimulus; it would seem more probable that its growth hastens

the setting in of conditions under which sexual organs can develop on the other vegetation, possibly by removing inhibiting substances. Measurements show that oospores of a size characteristic of the *parasitica* strain, when grown in pure culture may develop on its vegetation in the paired cultures. The finding of oospores in pure cultures of any of the strains of *P. palmivora* would give full force to Lester-Smith's view. It has been mentioned that the antheridia are always amphigynous and the sexual organs apparently always borne on different hyphae which cannot be traced definitely by direct observation either to the one or the other mycelium. Examples have been found in a number of cultures where the antheridium and the oogonium appeared to arise from one hypha as Dastur (20) described in *P. parasitica*, but in view of Murphy's (19) observations on *P. erythroseptica* and his comment on Dastur's interpretations, they have not been regarded as significant. Clinton (21) was the first to grow two members of the genus in paired cultures—*P. infestans* and *P. Phaseoli*; oospores were formed in the "infestans" zones which he interpreted as hybrids, but as Murphy pointed out they could more reasonably have been regarded as oospores of *P. infestans*.

I have recorded (18) the presence of large oospores in the zone of *P. Cinnamomi* Rands in a paired culture of it with *P. parasitica* (microspora). Oospores were also found to have formed freely in the growth-zone of two strains of *P. cryptogea* after ten days at 23° C. on maize-meal agar, which were growing in paired culture with *P. Cinnamomi*. Oospores which were restricted to the "cryptogea" vegetations showed a mean size for fifty of 23·6 and 24·6 μ respectively, and were very similar in size and development to those recorded by Pethybridge and Lafferty (38) as occurring in pure cultures of *P. cryptogea* after several months. In the present instance pure cultures of the two strains of *P. cryptogea* failed to show the presence of oospores after a month's growth. In these instances the presence of another species in the culture hastened the onset of conditions under which sexual organs could develop on a bisexual mycelium, and it is probable that other instances of the same effect could be found in the genus.

The strains placed in the "cacao" group on the basis of their behaviour in the mixed cultures are characterised by relatively broad sporangia and large chlamydospores, as Gadd observed in his Ceylon isolations. A number of the strains in the "rubber" group have narrower sporangia and smaller chlamydospores, as he also observed, but the strain from *Mimusops* sp. in the Gold Coast and from citrus in the Philippines have sporangia at least as broad as any strain in the "cacao" group, while the Philippine coconut and cacao isolations have chlamydospores which are

larger than those of any strains in the "cacao" group. A grouping based on the character of the asexual spores in single strain cultures, therefore, would not correspond, for the species as a whole, with a grouping based on the presence or absence of oospores in mixed cultures.

The isolations made from cacao pods in the West Indies, South America, West Africa and Ceylon can be definitely placed in the "cacao" group, and it is probable that they constitute a single strain which, of all those known, is alone able to infect unwounded cacao pods. Reinking's (8) isolation from a single cacao pod at Los Baños in the Philippines, appears to be an exception as it belongs in the "rubber" group. He, however, did not record infection experiments with it on unwounded cacao pods and his isolation from the coconut which was morphologically identical with the cacao isolation, was found to be only a weak wound parasite on cacao pods. It is not known, therefore, if his isolation from cacao was the strain normally responsible for pod rot in the Philippines, or merely an accidental wound parasite. Ocfemia and Roldan (4) recorded infection of cacao pods in the Philippines by their isolation from citrus, but furnished no details and did not state if the pods were unwounded. In an intensive study of cacao pod rot in one locality in the Gold Coast, Dade (22) has recorded that the great majority of the infections due to this species of *Phytophthora* seemed to occur on unwounded pods, an indication that only the strain which can infect through the uninjured surface is likely to be of economic importance on cacao. The isolations from bud rot of the coconut in Jamaica and from the coconut and Sabal palm in Porto Rico appear to be the same strain, from which the isolation from the coconut in the Philippines differs only in producing rather larger chlamydospores; all are members of the "rubber" group. The isolation from the coconut in India, on the other hand, is a member of the "cacao" group and therefore a distinct strain from that in the West Indies and the Philippines. Gadd found the strain on the coconut in Ceylon also to behave as a member of the "cacao" group and resemble the cacao strain morphologically, and although he has not recorded measurements of the asexual spores (a culture has not been available) it seems highly probable that it is the same strain as that on the coconut in India. It has been mentioned that the Indian strain is, in culture, quite typical of the species; the sporangia, which are very regular in form on the standard media, are rather larger than those of the cacao strain but of very similar ratio; the chlamydospores are like those of the cacao strain in size but are more frequently terminal than in the latter strain; evidence has also been furnished in Table V that the oospores may be larger.

Nomenclature of the species.

Butler was the first to name the strain on palms in India. In 1907 he described it (12) under the binomial *Pythium palmivorum* on the natural substrata—the palmyra (*Borassus flabellifer*) and the coconut in Madras, and added further details in 1910 (23). It was isolated in pure culture for the first time by Shaw and Sundararaman (24) in 1914 and again by McRae (25) in 1923, but none of these observers recorded its cultural characters. In 1919 Butler (26) transferred it to the genus *Phytophthora* as *P. palmivora*. In his original description Butler called the bodies oospores which are now commonly known as chlamydospores, but recognised their asexual character in 1910; his description and drawings of the sporangia and chlamydospores as they occurred on the hosts (Tables III and IV) agree very well with the character of those bodies in culture (*l.c.*).

The strain on cacao was recognised for the first time by Massee (27) in 1899, who referred it to *Phytophthora omnivora* de Bary. In 1909 von Faber (13) described it on cacao pods (not in pure culture) from the Cameroons and as Petch had already done, doubted the correctness of Massee's determination but did not give it a new name. In the same year (1909) Maublanc (28) published the binomial *Phytophthora Faberi* with a short diagnosis based on von Faber's data. It was reported for the first time in authentic pure culture in 1910 by Rorer (29) in Trinidad who isolated it from cacao pods and bark, and by Coleman (14) in Mysore, who isolated it from cacao pods sent to him from Ceylon. Coleman proposed for it the binomial *P. Theobromae* but withdrew it on recognising the priority of Maublanc's name. He, as von Faber and Maublanc had done, mistook the chlamydospores for oospores. Subsequent isolations from cacao, whether in the West Indies, West Africa or East Indies, have been referred to *P. Faberi* Maubl. and Rosenbaum (11) studied the cacao strain in pure culture under that binomial in 1917.

In 1919 Reinking (30), finding an isolation from the coconut palm in the Philippines morphologically indistinguishable from an isolation made from a cacao pod, referred the strain on coconut in that territory to *P. Faberi*; this observation caused Butler (31) to express a doubt later in the same year whether *P. Faberi* and *P. palmivora* could be regarded as distinct species, and in 1924 (32) he took the view that they were not distinct; the author (16) shared this view but considered the form on palms and that on cacao in the West Indies as morphologically and biologically distinct strains. The same view has been stressed by recent observers, especially by Tucker (10), Gadd (1, 5), Lester-Smith (17) and Leonian (33).

In 1927 Gadd (5) recorded the isolation of a strain from the coconut in Ceylon which he found to agree in all essential characters with the isolations from cacao and other hosts which he had referred to *P. Faberi*. He found this Ceylon coconut strain to be only a very weak wound parasite on cacao pods, behaving in that respect like the isolations from palms in the West Indies and the Philippines. The absence of any record of the cultural character of the Indian palm strain in comparison with those of isolations from cacao, left some doubt as to the specific identity of *P. palmivora* and *P. Faberi*. This doubt can no longer exist and as Butler's binomial antedates Maublanc's (by two years) the latter's must be abandoned and all strains be referred to *P. palmivora* Butler with *P. Faberi* Maubl. and *P. Theobromae* Colem. as synonyms. As emended to include characters shown in culture it is an omnivorous tropical species of wide distribution, existing as a number of morphologically, and in some instances, pathologically distinguishable strains. On such standard media as bean-meal, quaker oats, and maize-meal agars typical cultures spread rapidly (optimum for growth 27–28° C. (8)) giving rise to a moderate aerial mycelium of sparingly branched hyphae 4–8 μ in diameter and forming, in less than a week at a mean temperature near 25° C., abundant large terminal prominently papillate sporangia in well-developed sympodia ((8), Pl. IX *C* and *D*): the sporangia when mature fall away from the sporangiophores by natural abscission with a short, often stout and more or less occluded pedicel. In water ten to forty or more zoospores are discharged depending on the size of the sporangium (34): in cultures on the standard media, sporangia have a mean length between 40 and 60 μ and a mean breadth between 25 and 35 μ with a mean ratio between 1·4 and 2·0, but are frequently appreciably smaller ((1) and Table III) on the natural substrata. Spherical and subspherical chlamydospores, terminal or intercalated, which do not separate by natural abscission (resting conidia, sphaeroconidia) also form quickly and abundantly (especially on oat and maize media); they have thin or thick, hyaline or brown walls and granular contents and germinate by hyphae; in mean size they range from 32 to 42 μ. In atypical cultures formation of sporangia may be more or less suppressed but chlamydospores are developed freely. When young mycelium from either typical or atypical cultures is brought into water, sporangia are usually formed freely in sympodia at temperatures between 20° and 30° C. in two to three days. Sexual spores have not been recorded hitherto in single strain cultures and in only one instance (7) on the host (the coconut in Jamaica). Amphigynous sexual organs with oospores having a mean diameter between 22 and 24 μ are,

however, formed freely within a week on maize-meal agar at moderate temperatures (20–25° C.) when suitable strains are grown together in pairs. The strains can be divided into two groups conveniently named the "cacao" and "rubber" groups on the basis of this behaviour; oospores are formed within a few days when a member of one group is grown with a member of the other but have not been detected after three to six months when two members of one group are grown together. This reaction if it occurs promptly can be used as a means of identifying a new isolation if it has not been found to form oospores in pure culture.

It should be grown in paired culture on maize-meal agar between 20° and 25° C. with a known strain of each group and the intervening zone between the inocula examined for sexual organs after six to seven days; the inocula should be fragments of agar about 4 mm. in diameter taken from young cultures of similar age. If sexual organs are found in one paired culture but not in the other the latter should be examined again after a month; the absence of oospores after this interval would confirm the earlier data.

The evidence available indicates that the prompt development of oospores in paired culture with a strain of only one group of the species is the most reliable means of distinguishing between a pronounced atypical strain of *P. palmivora* and a strain of *P. parasitica* which develops oospores in pure culture only with difficulty. If oospores do develop in paired cultures with such a strain of *P. parasitica* they are found only after weeks or months and in the pairs with strains representing both groups of *P. palmivora*.

Inoculations on cacao pods.

Pure cultures of some of the strains of *P. palmivora* were sent to Mr H. A. Dade, Government Mycologist in the Gold Coast, who inoculated each of them on to ten detached pods of *Amelonado* and a like number of pods of *Criollo cacao*, half of which in each variety were wounded and half left unwounded; the pods were kept in large desiccators over water at a temperature varying from 75–82° F. Limitation of space allows of only a brief reference to the results (35). The strains from the coconut in Jamaica failed to infect unwounded pods and infected only one-fifth of the wounded pods of both varieties; the strain from the coconut in India also failed to infect unwounded pods, but caused a delayed (seven days) infection of two-fifths of the wounded *Amelonado* pods and four-fifths of the wounded *Criollo* pods. The strains from rubber in Malaya, cotton in St Vincent, *Mimusops* sp. in the Gold Coast, and citrus in the Philippines

failed to infect either wounded or unwounded pods of both varieties. The strain from cacao in the Philippines would not infect unwounded pods of either variety but gave a delayed infection (after ten days) on one-fifth of the wounded pods of both varieties. The Trinidad and Gold Coast cacao strains, which had been in culture for some years, readily infected wounded pods of both varieties but infected only one-fifth to two-fifths of the unwounded pods (the Gold Coast strain failed to infect unwounded *Criollo* pods), whereas a strain freshly isolated in the Gold Coast infected four-fifths of the unwounded pods of both varieties, indicating that the specialised ability of the cacao strain to infect the unwounded pod may be appreciably weakened but not readily lost in artificial culture. The pods of *Criollo* with thin and soft walls did not, in these trials, show greater susceptibility on the whole to infection than the pods of *Amelonado* with thick, hard walls. The *Mimusops* strain, which had been in culture for two to three years, failed to give a single infection but had been found by Dade to infect rather readily when freshly isolated. It is probable, therefore, that inoculations on cacao pods with strains of *P. palmivora* which have been in pure culture for some years may yield misleading results and that data should be sought only with relatively recent isolations.

These results and those recorded by Gadd (5), Tucker (9, 10), Reinking (30) and the author (36) show that the strains on the coconut are only weak to very weak wound parasites on cacao pods.

Inoculations made by Mr Dade at the same time on unwounded *Hevea* fruits and bolls of Egyptian cotton indicated that all the strains tested could infect readily. It is probable that any strain of *P. palmivora* will infect unwounded *Hevea* fruits and unwounded bolls of Egyptian and Sea Island cottons (37) and that the ability to do so is not lost readily in pure culture.

Additional Note

Since these notes were written, cultures have been received from Dr W. McRae, Imperial Mycologist in India, of an isolation made in 1925 from the bud-rot of the palmyra palm in the delta of the Godavari; sub-cultures on standard media show it to be a typical strain of *P. palmivora*. The sporangia are relatively somewhat narrower than those of the Indian strain from the coconut; McRae (*Ann. Rept. Agric. Res. Inst. Pusa*, p. 53, 1926–7) has recorded the mean size of four hundred sporangia on oatmeal agar as $55 \times 33\mu$ (ratio of 1·67). In paired culture on maize-meal agar with strains of the "rubber" group, oospores develop within a few days, but none have been found in paired cultures with strains of the "cacao" group; it behaves therefore, like the isolations from the coconut in India and Ceylon and must be included in the "cacao" group.

Reference has been made, in the body of the paper, to the probability that oospores would be found sooner or later in pure cultures of strains of the species; the statement by C. M. Tucker (*Ann. Rept. for* 1927, Porto Rico Agric. Exper. Stat.), which follows, is therefore of interest: "Examinations of oatmeal agar

cultures kept out-of-doors at Columbia, Mo., during the winter, revealed the presence of oogonia and oospores in two strains of *Phytophthora palmivora*." Atypical cultures of these strains were kindly sent to me by Mr Tucker who stated that they had been grown from single hyphae or single spores. Sexual organs with amphigynous antheridia and oospores, varying in mean size from 22 to 24μ, were fairly abundant in the cultures, on bean-meal agar, of one strain (descended from Reinking's isolation from the coconut in the Philippines), but scanty in those of the other strain (descended from Stahel's isolation from cacao in Surinam). When grown in paired culture, these strains behaved like those of the same origin which I had examined already, one falling into the "cacao" group and the other into the "rubber" group. Oospores have been detected in cultures eight months old on bean-meal agar which were grown from hyphal tips of the Philippine isolations sent by Mr Tucker.

I am much indebted to Messrs C. M. Tucker (Porto Rico), G. O. Ocfemia (Philippines), A. Thompson (Malaya), the Directrice, Centraalbureau voor Schimmelcultures, the Curator, Type Culture Collection, Lister Institute, for cultures; to Mr H. A. Dade (Gold Coast) for cultures and for undertaking inoculations; to Miss E. Hellinger for the measurements of the oospores in a number of cultures and to Mr G. Atkinson for enlarging the figures.

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TWO DOWNY MILDEWS OF THE NETTLE: PSEUDOPERONOSPORA URTICAE (LIB.) SALM. ET WARE AND PERONOSPORA DEBARYI NOMEN NOVUM.

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(With six Text-figures.)

1. Systematic.

In 1925 we pointed out that *Peronospora Urticae*, germinating by zoospores, should be transferred to the genus *Pseudoperonospora*. In 1926, in the course of further work, we found that a second downy mildew on the Nettle, germinating by a germ-tube, existed. It became necessary, therefore, to review criti-

cally the information on *Peronospora Urticae* given in mycological literature, and to examine the material available in herbaria.

In 1846 Berkeley, in his observations on the "Potato Murrain," wrote in describing *Botrytis infestans* Mont.—now *Phytophthora infestans*—"The peculiar characters of the species consist in the few erecto-patent not forcipated or uncinated branches, the scattered spores and above all the torulose swellings which give it somewhat the appearance of *Gonatobotrys*. The spores however are not disposed round the knots as in that genus and *Arthrobotrys*, or even confined to them. The only species which exhibits anything of the kind is the one which has been named *Botrytis Urticae* by Mlle Libert, and which indeed M. Desmazières considered as identical. It appears to me however that it is quite distinct, the flocci being far more divided, the apices bifid, and the colour, instead of white, a greyish lilac. I have had the opportunity, fortunately, of comparing specimens, which occurred in the autumn, at Tansor, in Northamptonshire, with authentic individuals from M. Desmazières."

In 1851 Berkeley and Broome gave a fuller description of the fungus on the Nettle, as follows: "*Botrytis Urticae* Libert MSS. On leaves of the common nettle, Tansor, Norths. Patches small, orbicular, greyish lilac, flocci loosely divided above, branches forming an acute angle, extreme ramuli simple or forked, sometimes curved, very rarely inflated. Spores large, ovate, apex papillaeform. Allied to the last [*Botrytis infestans* Mont.*] but distinct. When the flocci are ruptured, the inner membrane sometimes protrudes, as in the asci of *Sphaeriae*."

In 1855 Caspary transferred the species to the genus *Peronospora*, without giving any description.

In 1860 Berkeley, in *Outlines of British Fungology*, placed the species in *Peronospora* under the name *P. Urticae* Casp.

In 1863 de Bary, in his monographic study of the group, published the following account of a downy mildew on *Urtica*: "*Peronospora Urticae* (Lib.); *Botrytis Urticae* Libert MSS. apud Berkeley, Journ. Hort. Soc. Lond. 1, p. 31. Berkeley et Broome, Notices on Brit. Fungi, in Ann. Mag. Nat. Hist., ser. 2, vol. VII, p. 100.—Stipites conidiferi humiles, laxe 4–6-ies dichotomi; rami flexuosi, ultimi subulati arcuati saepe deflexi. Conidia magna, late ovoidea vel subglobosa, distincte pedicellata, apice obtusissima, membrana dilute violascente. Oosporae mediocres, episporio sordide fusco.—In Urticae urentis L. foliis legi, in agro francofurtano. In Gallia et Anglia a cell. Desmazières et Berkeley ('On leaves of the common nettle') lecta est. Rara esse videtur in Germania australiore, saltem frustra saepe quaesita est. Caespites conidiferi maculiformes, densi, humiles,

* Now *Phytophthora infestans*.

pallide violascentes, in foliorum pagina inferiore proveniunt. Stipites conidiferi illis *Peronosporae effusae* valde similes sunt. Descriptio a cell. Berkeley et Broome l.c. data ad nostram non quadrat. Specimina gallica et anglica non vidi; icone autem visa, quam ad specimina Desmazieriana cel. Berkeley delineavit et cum Casparyo in litteris communicavit, non dubito fungum meum, speciem Libertianam et Berkeleyanam revera sistere."

The species was included by de Bary in his section *Pleuroblastae,* defined as follows: Conidia non papillata, membrana circumcirca aequali hyalina aut violascente praedita, germinando tubum simplicem et aliquo superficiei puncto, plerumque ex latere, protrudentia.

As we shall show later, the species described by de Bary differs *in toto* from the fungus described earlier by Berkeley. Let us first confine our attention to Berkeley's species as determined by the herbarium material available. Berkeley stated (1) that this species had "been named" *Botrytis Urticae* by Libert. No indication is given by Berkeley that Libert ever published a description, and his use of the name "*Botrytis Urticae* Libert MSS." in 1851 would seem to show that he believed that it existed in manuscript only. We have not been able to trace any publication of the name or description of the fungus by Libert, nor have we been able to learn of the existence of any type specimen of *Botrytis Urticae* in Libert's herbarium deposited at the Jardin Botanique de l'État at Brussels. In response to our enquiry, Professor E. Wildeman kindly made a search but has been unable to find a specimen labelled *Botrytis Urticae*.*

Berkeley's herbarium at Kew contains a specimen labelled, in Berkeley's handwriting: "*Botrytis Urticae* Libert. M. Desmazières. Lille." On this sheet is a drawing, made by Berkeley, showing clearly the rigid branching of the conidiophore and the oval, minutely papillate, conidium. We have examined this fungus, which agreed perfectly with the drawing, and obtained the following measurements: Conidium: $27 \times 18\,\mu$, $28 \times 18\,\mu$,

* Professor E. Wildeman was good enough to send us two specimens from Libert's herbarium, labelled respectively, in Libert's handwriting: "*Oidium ? species nova*" and "*Oidium Urticae* N. hypophyllum caespitibus rotundis demum confluendo sat expansis floccis erectis ramosis albis articulis dilabentibus ovali-oblongis didymis ? an hujus generis. In foliis vivis Urticae dioicae. Autumno." The second specimen is mounted on a sheet labelled "Peronospora urticae (Lib.) de Bary," to which has been added, in pencil, "f. Delogne." The fungus in both these specimens is *Ramularia* and obviously has nothing to do with the fungus called *Botrytis Urticae* by Libert.

In the hope of learning of the existence in Desmazières' herbarium of a specimen of *B. Urticae,* labelled or collected by Libert, we wrote both to Paris and Lille. Professor E. Foëx has informed us that after a search made by him and M. Biers at the Museum (Paris), no specimen of *B. Urticae* could be found there in Desmazières' herbarium, in that of Montagne, in Libert's Reliquiae mycologicae, or in the general herbarium. The Curator of Cryptogams, of the Faculty of Sciences of Lille, has informed us that they possess only the Exsiccati published by Desmazières, in which no example of *B. Urticae* occurs.

32 × 20 μ, 25 × 18 μ, 33 × 22 μ. Oospore (globose) diameter 30 μ, 28 μ, 34 μ. The host plant is *Urtica dioica*.

The above material doubtless represents the "authentic individuals from M. Desmazières" to which reference is made by Berkeley in his original description in 1846. There is no evidence that this fungus was collected by Libert, but in the absence apparently of any type specimen in Libert's herbarium, we have to rely on this identification by Desmazières. In Berkeley's herbarium also, is a specimen labelled (in Berkeley's handwriting) "*Botrytis Urticae* Libert. Tansor 1845." This fungus, on *Urtica dioica*, has conidia minutely apiculate and borne on conidiophores with rigid, non-flexuose branches. It is clearly identical with Desmazières's specimen. Another example of the fungus exists in Broome's herbarium at the British Museum (Natural History), and is labelled "*Botrytis Urticae* Lib. Tansor, Northampt^n. 1845 ex herb. M.J.B." Two conidia, minutely apiculate, measured 29 × 18 μ and 28 × 18 μ.

Turning now to the diagnosis given by de Bary of his *Peronospora Urticae*, we find that in place of the "ovate" conidium, with "apex papillaeform" of Berkeley's *P. Urticae*, we have the "broadly ovoid or subglobose" conidium, with apex "very obtuse." It is not surprising then that de Bary remarked that Berkeley and Broome's description of their species did not agree with his. De Bary himself explains that in spite of this obvious discrepancy he used Berkeley's name because he saw a drawing, made by Berkeley, on specimens collected by Desmazières, which had been sent by Berkeley in a letter to Caspary, and this drawing convinced him that his species was in very truth ("revera") the same as that of Libert and of Berkeley*.

De Bary, then, considered the evidence furnished by this drawing of greater importance than the characters given in Berkeley and Broome's diagnosis. After de Bary's pronouncement that his *Peronospora* with very obtuse conidia was really identical with Berkeley's *Peronospora* with apiculate conidia, all systematists for the next sixty-five years followed him in misapplying Berkeley's name. As a result, Exsiccati sent out contain two perfectly distinct species under the name *Peronospora Urticae*.

Out of this misunderstanding, a new entity soon appeared—a fictitious compound arising from the confusion. Cooke, in 1865, under *Peronospora Urticae* Casp., described the conidia as "large, broadly ovoid or subglobose...apices very obtuse"—the diagnosis being obviously copied from de Bary. Cooke then adds: "On leaves of the Common Nettle," whereas de Bary's

* One is led to speculate whether possibly Berkeley sent to Caspary a drawing in which the shape of the conidium was not so clearly indicated as on the specimen in his herbarium at Kew.

species was described from examples on *Urtica urens*, on which species alone it occurs. In 1871, Cooke, in his *Handbook of British Fungi*, describing *P. Urticae* Casp., quoted references both to de Bary and to Berkeley and Broome and gave a diagnosis consisting, first, of that given by de Bary ("acrospores large, broadly ovoid or subglobose...apices very obtuse") and then of that of Berkeley and Broome ("acrospores large, ovate, apex papillaeform"). No doubt Cooke was puzzled—as we are to-day—by de Bary's pronouncement on the subject, and perhaps he did the best that was possible at that time by giving without comment, under the one species, the two diagnoses.

Massee, in his *Phycomycetes and Ustilagineae* (1891), described *P. Urticae* de Bary as having "broadly elliptical or subglobose" conidia with the apex "very obtuse," and adds: "Cooke says that the gonidia [conidia] have the apex papillaeform, but very obtuse." In this last sentence we reach the depth of the confusion*.

In 1888 Berlese and de Toni, in Saccardo's *Sylloge Fungorum* (6), in describing *P. Urticae* (Lib.) de Bary†, give de Bary's diagnosis ("conidiis...apice obtusissimis") and the size of the conidia as 22–26 × 17–20 μ. References are given to de Bary, Berkeley and Broome, and Cooke. This fictitious species is stated to occur on *U. urens* and *U. dioica* in France, Belgium, England, Germany and North America‡.

In 1898 Berlese, in his *Icones Fungorum*, described *P. Urticae* (Lib.) de Bary as having "conidia broadly ovoid or subglobose," and the measurement of the conidium is given as 20–27 × 18–22 μ, and that of the oospore as 30–32 μ. In Tab. LXIII the conidium is represented as broadly ovoid, very obtuse at the apex and with no apiculus. It is stated that this plate was drawn from the specimens sent out in Linhart's Fungi hungarici, No. 487, and compared with many others. We have examined the fungus in Linhart's Exsiccati and found it to be de Bary's species; Berlese's Tab. LXIII well illustrates the spore with its very obtuse apex. References are however made to Berkeley and Broome, and probably on this account *Urtica dioica* is inaccurately given as a host-plant.

In 1904 Berlese, in his "Saggio di una Monografia delle Peronosporacee," gave the same diagnosis with very similar drawings, quoting the following Exsiccati: Fuckel, Fungi Rhen.

* The same confusion is shown in Massee's *Diseases of Cultivated Plants and Trees* (1910), p. 110, where it is remarked that the "broadly elliptical" conidia "have generally a suggestion of a papilla at the apex."

† As we have previously pointed out (17), Caspary and not de Bary was the first to place the present species in *Peronospora*.

‡ We are not attempting to deal in the present paper with the records of *P. Urticae* from America.

1510; Thuem, Myc. univ. 345; Linhart, Fungi Hungar. 487; Rabenh., Fungi Eur. 1665; Schneider, Herb. Schles. Pilze, n. 36, 270. With the exception of the last named, we have examined examples of all the above Exsiccati in the British Museum (Natural History) London and can state that the fungus is in each case de Bary's species with non-apiculate conidia, and in every instance the host plant is *U. urens*. From the above it is clear that the species known to Berlese as *P. Urticae* was de Bary's and not Berkeley's species.

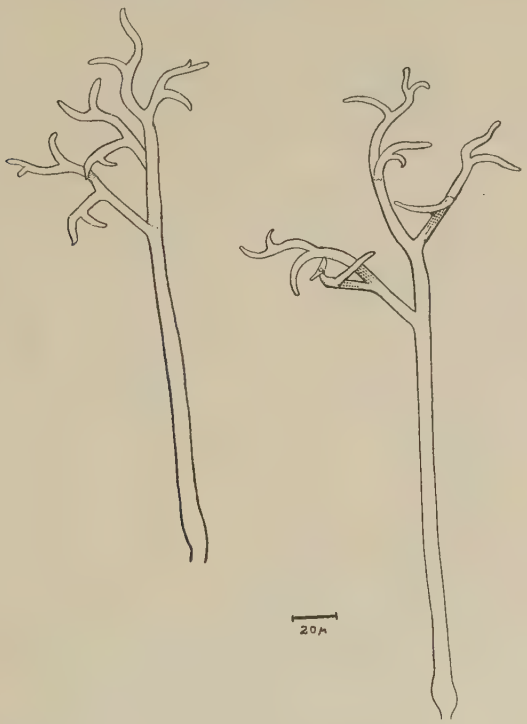


Fig. 1. *Peronospora de Baryi.* Conidiophores. (× 250.)

Fischer, in 1892, described *P. Urticae* (Lib.) de Bary as having conidia "breit eiförmig, stumpf, durchschnittlich 20 μ breit, 26 μ lang," and as occurring on *U dioica* and *U. urens*, but more frequently on the latter. Since, so far as we know, de Bary's species with non-apiculate spores occurs only on *U. urens*, it would appear either that Fischer did not notice the different conidial characters of the fungus occurring on *U. dioica*, or that he added this host species because he found it given in Berkeley's account, to which he refers.

Migula, in 1910, under the name *P. Urticae*, described the

conidia as "kurz eiförmig, stumpf, etwa 20 μ dick, 26 μ lang"; this description fits de Bary's species, but again the host plants are given as *U. dioica* and *U. urens*.

In 1923 Gäumann's important work "Beiträge zu einer Monographie der Gattung *Peronospora*" appeared. In his treatment of *P. Urticae* Gäumann relies on de Bary for the specific diagnosis and gives a figure showing a conidiophore with flexuose branches and subglobose conidia with very obtuse non-apiculate apex. He gives *Urtica urens* as one of the host plants and under

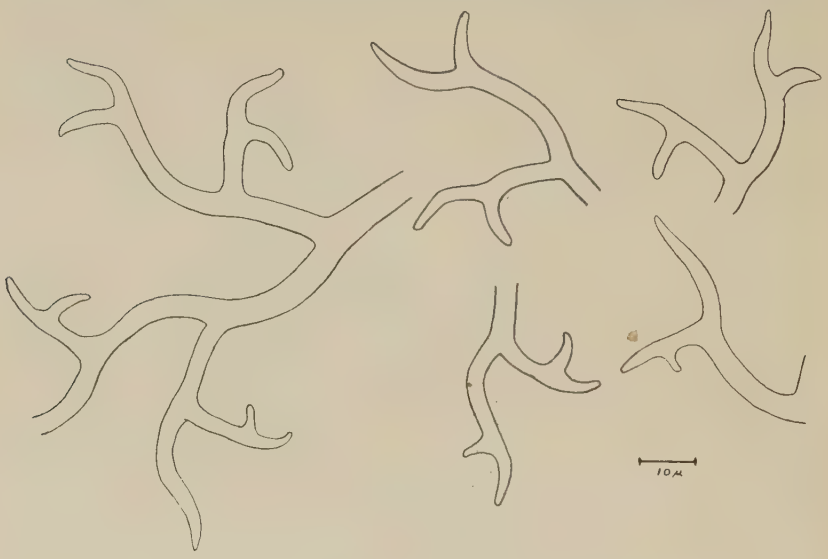


Fig. 2. Ultimate branches of the conidiophore. (× 750.)

this host plant quotes eight Exsiccati all of which (except one, viz. Roumeguére F. sel. exs. 4256) we have seen and found the contained fungus to be de Bary's species. Gäumann also gives *Urtica dioica* as a host plant and quotes Vestergren, Microm. rar. sel. 1672, as the material on which he bases the statement. We have examined the example in this published set in the Herbarium of the British Museum (Natural History) and can state that the fungus here is certainly the true *P. Urticae* and not de Bary's species. The conidiophores have non-flexuose branches and the conidia are ovate or oval, with a distinct apiculus*. As we have noted above, we have not met with de Bary's species on any host but *U. urens*, although *P. Urticae* occurs on both *U. dioica* and *U. urens*.

* Dr Gäumann has kindly sent us an example, labelled *P. Urticae* (Lib.) de Bary, collected by him "on *Urtica* (*urens*?), Siders (Wallis) 7 Sept. 1924." Here again the fungus is de Bary's, and not Berkeley's, species.

In 1925 we pointed out the close morphological resemblance of the conidial stage of a Downy Mildew which we found at Wye on *Urtica dioica* and on *U. urens* with that of *Pseudoperonospora Humuli* (Miy. and Takah.) Wils., and made a comparative study of the two. From the diagnostic characters given (3), we referred the Nettle Downy Mildew to Berkeley's species but had no suspicion at the time that the name *P. Urticae* was being used by many writers for another totally distinct species. As the result of the measurement of 105 conidia, the average size was found

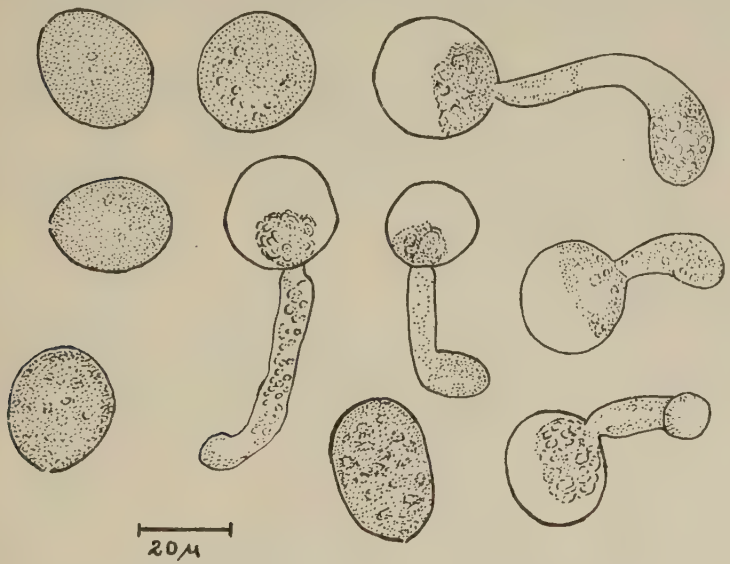


Fig. 3. Conidia, showing mode of germination. (× 600.)

to be 27 × 18 μ, with the limits for length 22–40 μ, and for breadth 14–22 μ*. The size of the five conidia found on the "authentic individuals from M. Desmazières" in Berkeley's herbarium (see above, p. 40) falls well within the limits. The conidium in all our specimens showed the oval shape and the small apiculus, as depicted in Berkeley's drawing referred to above (p. 40). As regards the size of the oospore, we found this to average, from 80 measurements, 30 × 29 μ, the limits of both length and breadth (for oval and globose spores) being 16–38 μ†. Here again the size of the three oospores observed in Desmazières's specimens is in accordance.

In our investigations in 1924 (17) we discovered that the coni-

* Blattny gives (7, pp. 153, 157) the size of the conidia of *P. Urticae* as 29·25 × 21·25 μ on *U. dioica* and 28 × 20·5 μ on *U. urens*.

† Blattny (p. 156) gives the size of the oospore as averaging in one case 27 × 26 μ, and in another 29 × 28·5 μ, the limits of size being 19–37 μ.

dium germinates by means of zoospores and on this account we removed the species from the genus *Peronospora* to *Pseudoperonospora*. It was not until 1926 that we first met with and had the opportunity of studying living examples of the second species of Downy Mildew which occurs, as far as we know, on *U. urens* only. We first found this on September 24th, 1926, in a hop garden near Wye on plants of *U. urens* growing thickly between the rows of hops. The branches of the conidiophore were flexuose and not so straight as in *P. Urticae* (Fig. 1); the conidia were broadly ovoid or subglobose, with no apiculus (Fig. 3) and measured 24–31 × 21–24 μ, the average of twenty conidia being 29 × 23 μ. When placed in water, the conidia germinated readily within twelve hours by the production of a germ tube. The haustoria, as observed in the stem and petioles, were vermiform and either simple or, more commonly, bifurcate (Fig. 5).

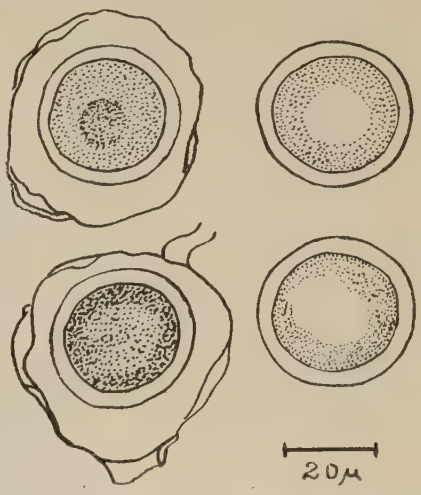


Fig. 4. Oospores. Two are still enclosed in the remains of the oogonium. (× 600.)

On October 2nd, 1926, the same fungus was found, on plants of *U. urens*, growing in great profusion in an apple plantation near Marden, Kent*. The shape of the conidiophore, conidium and haustorium agreed with that of the fungus previously found at Wye. One hundred measurements of conidia were made; the limits of length were 23–32 μ and of breadth 19–24 μ. The average size was 28 × 22 μ and the mode was the same.

On November 8th, 1927, the plantation near Marden was revisited and the species was found again plentifully on *U. urens*. In some of the plants examined oogonia and oospores were present in the curled and brown tips of conidiophore-infested leaves of the lateral shoots. The size of the oogonium† in six examples was 44–55 × 43–50 μ, and thirty oospores‡, globose in shape, with thick, smooth, colourless walls, measured 30–36 μ. One hundred conidia were measured and the average size was

* At the edge of the plantation, *U. dioica* occurred, attacked by *Pseudoperonospora Urticae*.

† One oogonium was seen which measured 60 μ, and contained an oospore of 34 μ diam.

‡ One oospore measured 39 μ; it was still enclosed by the oogonium which measured 50 μ.

found to be 27 × 23 μ. The variation was 23–30 × 20–25 μ, and the mode 28 × 22 μ.

On reference to systematic literature, and by the examination of authentic specimens, we found, from Berkeley and Broome's diagnosis, that we had been correct in using the name *Peronospora Urticae* for the apiculate-spored species, which we had transferred in 1925 to *Pseudoperonospora*. It became clear to us also that the second species we were now studying was that described as *Peronospora Urticae* in 1863 by de Bary under the mistaken assumption that it was Berkeley's species. We propose to give this latter species the name of *Peronospora*

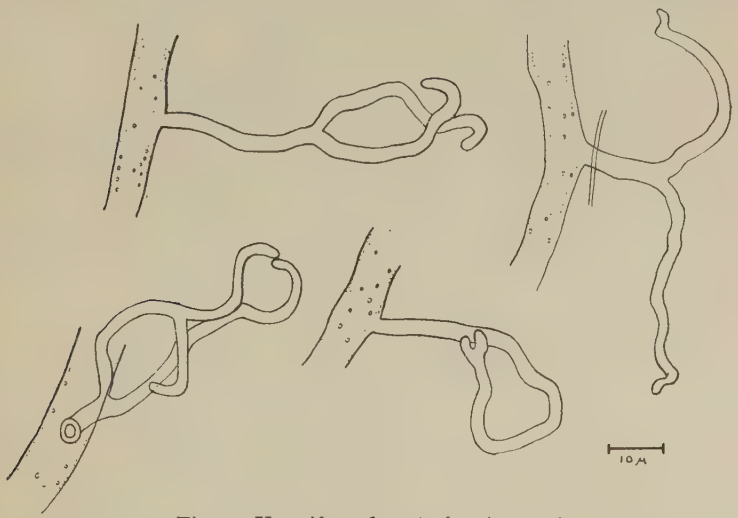


Fig. 5. Vermiform haustoria. (× 700.)

deBaryi, in view of the fact that this author was the first to describe its characters. The chief diagnostic characters of the two species are as follows:

Pseudoperonospora Urticae. Caespites conidiferi griseo-violacei; conidiophori ramis non flexuosis rigidis; conidia elliptica 22–40 × 14–22 μ, plerumque 27 × 18 μ, apice minute apiculata; oosporae globulosae 16–38 μ diam., plerumque 30 × 29 μ.

Peronospora deBaryi. Caespites conidiferi albidi vel pallide griseo-violascentes; conidiophori ramis flexuosis; conidia late ovoidea vel subglobosa, apice obtusissima, non apiculata, 23–32 × 19–25 μ, plerumque 28 × 22 μ; oosporae globulosae 30–39 μ diam.

The synonymy is as follows:

Pseudoperonospora Urticae (Lib.) Salm. et Ware. *Ann. App. Biol.* XII, 141 (1925).

Botrytis Urticae Lib. MS. Berk., *Journ. Hort. Soc. Lond.*

I, 31 (1846); Berk. and Broome, *Ann. and Mag. Nat. Hist.* ser. 2, VII, 100 (1851).

Peronospora Urticae (Lib.). Caspary in *Ber. Verhandl. Königl. Akad. d. Wissensch. Berlin* 330 (1855); Berk., *Outlines of Brit. Fungology* 349 (1860); Cooke, *Rust, Smut,* etc. 216 (*pro parte*) (1865); *Handbook Brit. Fungi* 595 (*pro parte*) (1871); Massee, *Phycomyc. and Ustilag.* 124 (*pro parte*) (1891); *Mildews, Rusts and Smuts* 34 (*pro parte*) (1913).

Peronospora deBaryi nomen novum.

Peronospora Urticae de Bary (*synon. exclusis*). *Ann. sci. nat.* 4 sér., XX, 116 (1863); Berlese et De Toni in Sacc. *Syll. Fung.* VII, 257 (1888); Fischer in Rabenh. *Krypt.-Fl. Deutschl.* IV, 473 (1892); Berlese, *Ic. Fung.* 39 (1898); Berlese, *Riv. Pat. veg.* X, 269 (1904); Migula, *Krypt.-Fl. Deutschl.* III, 175 (1910); Gäumann, *Beitr. Krypt. Schweiz,* V, 302 (1923).

P. Urticae Caspary. Cooke, *Rust, Smut,* etc. 216 (*pro parte*) (1865); *Handb. Brit. Fungi* 595 (*pro parte*) (1871); Massee, *Phycomyc. and Ustilag.* 124 (*pro parte*) (1891); *Mildews, Rusts and Smuts* 34 (*pro parte*) (1913).

The distribution* of the two species, based on examination of Exsiccati and other specimens in our national Herbaria, is as follows:

Pseudoperonospora Urticae (Lib.) Salm. et Ware on *Urtica dioica.*

Exsicc. Vestergr., Micromyc. rar. sel. 1672; Krieger, Fungi sax. 1045; Cooke, Fungi Brit. ann. exsicc. 292. Sub *Peronospora Urticae.*

England; Tansor, Northamptonsh., 1845; Berkeley (Herb. Berkeley in Herb. Kew and Herb. Brit. Museum). Shere, Surrey, October 1866 M. C. Cooke. Scotland; West Kilbride, Ayrsh. July, 1897 leg. D. A. Boyd (in Herb. Brit. Mus.).

France; Lille (Desmazières), in Herb. Berkeley in Herb. Kew. Sweden; Stockholm. Germany: Königstein.

In addition to the above records we can add the following:

On *U. dioica*:

England; Kent, common near Wye 1925–1927 (Salmon and Ware); Middlesex, Twickenham, October 1924 (Salmon); Kent; Harbledown, near Canterbury, September 1926 (Ware). Scotland; Balgownie near Aberdeen, August 25th, 1886 (Herb. J. W. H. Trail)†.

* It appears probable that in Belgium both species occur. Lambotte (*Fl. Myc. Belge,* 97 (1880)) mentions a species on *U. urens* which from the description must be *Peronospora deBaryi,* and Bommer and Rousseau (in *Bull. Soc. Roy. bot. Belg.,* XXIII, (1884) 235) record a species on *U. dioica* which is doubtless *Pseudoperonospora Urticae.*

† In Trail's "Revision of the Scotch Peronosporeae" (*Scottish Naturalist,* III (1887–1888), 77), the following note occurs: *P. Urticae* (Lib.), "on *Urtica urens,* common. *U. dioica,* rare, once near Aberdeen, differing to some extent from the form on *U. urens.*" Trail appears therefore to have been the first

France; Grignon (coll. MM. Schad and Fourmont, July 1927). (Communicated by Professor Ducomet.)*

On *U. urens*:

England; Kent, near Marden, October 8th, 1924 (Salmon and Ware); Lincs., Haxey, September 5th, 1927 (H. H. Stirrup).

Fig. 6. *Urtica urens*. Upper portion of the main stem of a plant attacked by *Peronospora deBaryi*; the upper leaves and terminal bud have assumed a silvery yellow colour, the result of systemic infection. Collected Marden, Kent, November 8th, 1927. ⅔ nat. size.

We have not seen, either in Exsiccati or in herbaria, any examples of *P. Urticae* on *Urtica urens*. So far, two cases only to suspect that more than one species occurs on *Urtica*. Dr Gäumann has called attention (13) to Trail's opinion, and expressed disagreement. Dr Gäumann however, as we have noted above (p. 44), is unaware of the existence of one of the two species.

* Recent communication:—Czechoslovakia; Destnice, Saazer Gebiet, May, June, 1928 (Dr C. Blattny).

of the occurrence of this species on *U. urens* are known to us, the first, collected by us in 1924 near Marden, Kent, and the second, by Mr H. H. Stirrup, at Haxey, N. Lincs., in 1927. In an article now in the press, we record the results of certain inoculation experiments carried out by us in 1927 which show that *Pseudoperonospora Humuli* is able to infect, and form spores on *U. urens*. As we have already pointed out (17), the conidial stage of *P. Humuli* and of *P. Urticae* agree in their morphological characters. Since, however, we have found that the conidia of *P. Urticae* on *U. dioica* are able to infect fully *U. urens*, it may be assumed that the species found in nature on this latter host plant is *P. Urticae* rather than *P. Humuli*. It would, however, be of considerable interest to know of the existence of herbarium examples of *P. Urticae* on *U. urens* collected before 1920, so as to preclude the possibility of the fungus in question being *P. Humuli*, which was not recorded in Europe until that year*.

Peronospora deBaryi nomen novum.

Exsicc. Vestergr., Microm. rar. sel. 198; Linhart, Fungi hungar. 487; de Thuem, Myc. univ. 345; Fuckel, Fungi Rhen., 1510; Rabenh., Fungi Eur., 1665; Syd., Myc. March. 1347; Schneider, Herb. Schles. Pilze, n. 36; Sacc., Myc. Ital. 888; Krieger, Fungi Sax. 2128. Sub *Peronospora Urticae*.

Germany; Russia; Hungary; Italy.

In addition to the above records of *P. deBaryi* on *U. urens*, we can add the following:

England; Shropshire; Wellington, 1874. Herb. Wm. Phillips (Herb. Brit. Mus.). Kent; Wye, September 1926, 1927 (Salmon and Ware), Marden, October 1926, November 1927 (Salmon and Ware). Scotland; Old Aberdeen, August 23rd, 1886, Portsoy, August 17th, 1886 (Herb. J. W. H. Trail)†.

Switzerland; Siders (Wallis), September 7th, 1924 (leg. E. Gäumann). France; Grignon (coll. MM. Schad and Fourmont, July 1927). (Communicated by Professor V. Ducomet‡.)

Czechoslovakia; Carpathorussia, 1920 Dollia. (Communicated by Dr C. Blattny.)§

* It seems clear, from the specific characters mentioned by Blattny (7) that a *Pseudoperonospora* occurs in Czechoslovakia on *U. urens*. It is probable that this is *P. Urticae* rather than *P. Humuli*.

† We are indebted to Professor Craib, of the University, Aberdeen, for having kindly lent us these specimens.

‡ V. Ducomet (in *Rev. Path. vég.* XII (1925), 251), in combating our view of the morphological identity of the conidial stage of *Pseudoperonospora Urticae* and *P. Humuli*, has stated that *P. Urticae* clearly differs from *P. Humuli* in the shape and dimensions of the conidium. The explanation here is that he was probably dealing with *P. deBaryi* and not *P. Urticae*.

§ Recent communications:—England; Haxey, Doncaster (J. W. Ewan, Sept. 11th, 1928). Scotland; Edinburgh (Dr M. Wilson, July 1928). Moravia; Krumlov (Dr E. Baudyš, June 7th, 1928).

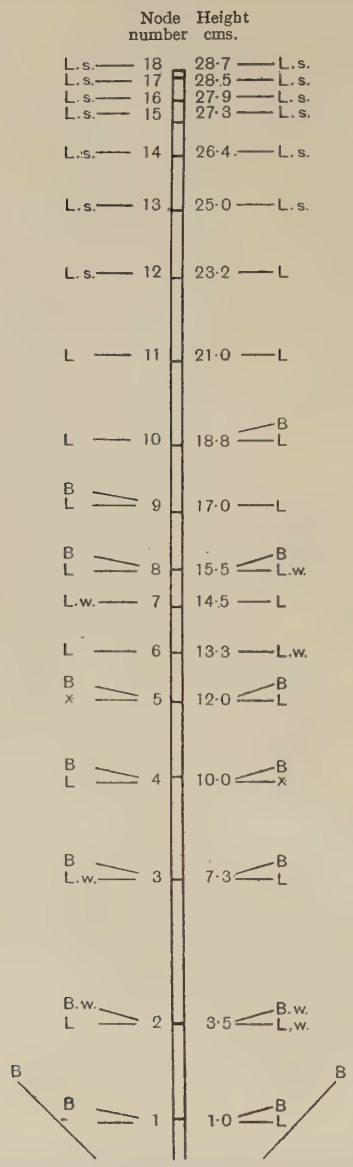
2. Biological.

The following observations concern the species *P. deBaryi* on *U. urens* which was first found in the open in a hop garden near Wye (Kent) on September 24th, 1926. The foliage of some of the annual nettles which were growing thickly between the rows of hops was of a bright silvery yellow at the tips of the main stems. With a lens, branched conidiophores were distinguished on the lower surface of many of these coloured leaves. The yellowing of the upper surface of the leaf was somewhat similar to that induced on other plants in the early stages of an attack of "red spider." The same colour on the lower surface of the leaf was often masked by a growth of conidiophores and conidia which was very pale grey with a scarcely perceptible violet tinge. In this respect the present fungus differed from *Pseudoperonospora Urticae*, which forms dark, greyish lilac masses of conidiophores and conidia. The discoloration at the tip of the main stem, or of its branches, involved about eight pairs of leaves covering a length of stem of approximately $2\frac{1}{4}$ inches. This and the general distribution of the fungus over the leaf surface, suggested systemic infection. Inflorescences in the axils of the yellow leaves were healthy and seeds were maturing.

It was further noted that the fungus occurred on isolated leaves and it was not by any means invariable that those symptoms which indicated systemic invasion of the whole apical portion of a shoot were present. When the fungus occurred on a leaf which on account of its colour could not be included amongst those described as systemically infected, it was present on the lower surface in small, usually angular patches of about 4 mm. diameter. Nearly as frequently it was found covering much larger areas which might extend from one end of the lamina to the other. The sides of these long areas were commonly bounded by the mid-rib or by the large veins on either side of the mid-rib. For example, on a leaf the lamina of which measured 46 × 40 mm., the fungus occurred on an area 46 × 13 mm.*, the long sides of the area being limited by the mid-rib and by one of the larger veins. The fungus itself was pale grey.

On the upper surface of the leaf the place of attack was very clearly defined by bright yellow-green which formed a sharp contrast to the dark green of the rest of the lamina and made it possible to distinguish from a distance most of the infected leaves. No brown or black discoloration of small areas of the lamina was seen, such as is typically caused by *Pseudoperonospora Urticae* on this host species.

* This was the widest space between the mid-rib and the other limiting vein.


Node number
Height cms.
L.s. 18 28·7 L.s.
L.s. 17 28·5 L.s.
L.s. 16 27·9 L.s.
L.s. 15 27·3 L.s.
L.s. 14 26·4 L.s.
L.s. 13 25·0 L.s.
L.s. 12 23·2 L
L 11 21·0 L
L 10 18·8 B L
B L 9 17·0 L
B L 8 15·5 B L.w.
L.w. 7 14·5 L
L 6 13·3 L.w.
B x 5 12·0 B L
B L 4 10·0 B x
B L.w. 3 7·3 B L
B.w. L 2 3·5 B.w. L.w.
B B - 1 1·0 B L B
Ground level

L. Leaf, normal.
L.s. Leaf, silvery.
L.w. Leaf, withered.
B. Branch, normal.
B.w. Branch, withered.
* Inoculated here.

Diagrammatic representation of a plant of *Urtica urens* two months after inoculation at the fourth and fifth nodes with *Peronospora deBaryi* nom. nov. Mycelium is present in the main stem from the apical bud to below ground level. For description see pp. 55–58.

Specimens with yellow leaves at the apex of the stem were taken to the laboratory and systemic invasion by the fungus was confirmed. In one plant seventeen inches high, with thick hypocotyl and the root extending a further three inches, the hyphae were traced by means of radial longitudinal sections, from the apical bud of the main stem to a position in the hypocotyl three-quarters of an inch below ground level, close to the beginning of the large white tap-root and at a place where lateral roots arose. The hyphae were plentiful in the pith and followed a longitudinal course on the periphery, very close to the primary xylem. Some mycelium was also found in the parenchyma of the secondary xylem. The haustoria were vermiform and were either simple or more commonly bifurcate.

Some of the fallen "seeds" were examined and one was found with conidiophores covering the perianth segments which appeared grey in comparison with the bright green perianths of other "seeds." The fruit (nut) was carefully removed from the perianth and was examined after maceration in Azo Blue. Quantities of mycelium, conidiophores and spores were found, and though a few conidiophores had been seen on the inside surface of the perianth segments, the fungus found on the fruit after it had been removed from the perianth, had actually been invading it and was probably producing conidiophores on the fruit itself.

The morphological characters of the conidia and conidiophores of *P. deBaryi* have been described above.

The disease was found persisting in the same hop-garden on October 17th and a further investigation of infected plants was made. In one typical plant, twelve inches high with tap-root three inches long, sections cut across the tip of the stem in the unthickened region showed hyphae situated between the collenchyma, which is grouped at the angles of the stem, and the vascular bundles. In the pith, hyphae were also present near the protoxylems. Mycelium was found in parenchyma tissue in the stem at ground level and in the hypocotyl region below ground. It was further traced into the tap-root and was present at a spot below the origin of lateral roots. In the root, the pitted vessels were invaded, as many as nine hyphae being found in one vessel. The parenchymatous tissues of the root were also generally invaded. The fungus was not present externally except on the leaves of the leading shoot for a distance of three and a half inches from the terminal bud.

One of the plants collected on October 17th was kept in water in the laboratory and was examined after five days. Oogonia were found in the wood-parenchyma and pith of the main stem. One oospore with colourless, smooth, thick wall (diameter 26 μ)

was still enclosed in the oogonium. Hyphae were also found in the lumen of pitted vessels in the main stem. In a few instances an antheridium was seen at the side of the oogonium but it was not possible to determine whether these arose from the same or different hyphae. The antheridia measured 14–16 μ in diameter and the oogonia (somewhat pressed out between the cell walls) measured 40–58 × 33–42 μ.

The following year (1927), on September 26th and 30th, further visits were paid to the hop-garden near Wye in which the fungus had first been found in 1926. Annual nettles were again plentiful and many of the plants showed the small yellowish leaves at the tips of main or lateral shoots. The length of stem bearing coloured leaves was from one to two inches and was considerably shorter than had been seen in the previous year. On this occasion, also, the leaves with isolated yellow spots or streaks caused by the fungus were extremely rare. Conidiophores and conidia occurred in dense grey tufts on the yellow leaves and were particularly grouped at the extreme tips of the marginal serrations. Some leaves were affected to such an extent that the margin was brown, dead and inrolled.

On November 8th, 1927, an apple plantation near Marden, in which the fungus had been found the previous year, was again visited. The disease occurred plentifully amongst the annual nettles which showed, however, only here and there the spotted or streaked leaves which had been so abundant in 1926. The yellow-coloured leaves at the tips of the stems (both main and lateral stems) were everywhere conspicuous. Some of the plants were brought to the laboratory and sections showed that there was a general systemic invasion, the mycelium extending from the apical bud through the whole length of the main stem (fifteen inches) but not into the hypocotyl or roots. Some of the laterals on a plant were systemically invaded whereas others were quite healthy. Of the two laterals at a node, it was common to find one diseased and one healthy.

On October 1st, 1927, inoculation experiments were made with conidia obtained from *Urtica urens*, collected on the previous day near Wye, in the hop-garden to which reference has already been made. The spores were taken up by means of a wet brush (previously cleaned by immersion in alcohol) and were placed in a watch-glass of distilled water. A drop of the suspension was placed on the leaf to be inoculated. Two leaves on each of five plants of *Urtica dioica* and two leaves on each of five plants of *U. urens* were inoculated, and, in addition, one leaf on each of five plants of both *Humulus lupulus* and *H. japonicus*. Spores were also placed in a drop of water on two slides which were kept in a damp dish. It was observed that ger-

mination on the glass slides was very slow and after two days only about one per cent. of the spores had produced germ-tubes. The inoculum must therefore be regarded as having been very weak.

All of the plants, except the Japanese hops (which were too large), were kept under bell-jars with a moist atmosphere and were given occasional ventilation daily. They were examined on October 8th and only on four plants of *U. urens* were any effects visible; the fifth plant and all the others (*U. dioica* and *Humulus* spp.) were thrown away.

The four annual nettles showed, on all of the eight leaves inoculated, large brown water-soaked areas confined by the larger veins. No conidiophores were present. Owing to there being such conspicuous effects on the inoculated leaves all of the plants were retained (uncovered) in a well-lighted position in the laboratory.

In order to discover whether there had been any penetration by the fungus, sections were cut on October 25th in the petioles of both the inoculated leaves on one plant. This plant, being not otherwise damaged, was kept for future examination. Both the laminae were then starting to wither. Hyphae, bifurcate haustoria, oogonia and oospores were found in the petioles. The size of three oogonia which were measured was $50 \times 40\,\mu$, and two oospores, still enclosed in oogonia, measured $30\,\mu$. One exceptionally large haustorium was seen which extended $20\,\mu$ into the host cell, and then branched into two vermiform parts each of which measured $50\,\mu$ in length. The thickness of the main axis of the haustorium was approximately $3\,\mu$.

Some of the older primary leaves of the main stem on all of the four plants became more or less withered in the course of the next month (November), but no symptoms of disease were noticed such as had been easily seen in plants growing naturally in the open. It was not until the end of the second month after inoculation (on November 30th), when the plants were being watered, that it was noticed with some surprise that the stems of all four had developed those silvery-yellow tips which were so well known as characterising systemic infection of *U. urens* in the open.

A close examination was made of one of the four plants which was the same as that from which the two inoculated leaves were removed for sectioning on October 25th. Notes were made of the symptoms and of the internal position of the fungus in relation to the symptoms. (Diagram, p. 52.) This plant was 28·7 cm. high and had eighteen nodes on the above-ground portion of the stem. One leaf of each pair at the fourth and fifth nodes had been inoculated, but they had already been removed (October 25th).

The bright silvery-yellow colour was visible on both the leaves at every node from the eighteenth down to the thirteenth; at the twelfth, only one of the pair showed this coloration. The length of stem bearing obviously discoloured foliage (nodes 12–18) was 5·5 cm. and this part of the plant was first examined. There were no conidiophores on any of the yellow leaves. Mycelium was plentiful in the petiole of the one silvery-yellow leaf at the twelfth node and oospores were crowded in the lamina, especially near the apex and in the apical serrations. They measured 30–39 μ and some were still enclosed in the oogonium. The other leaf at the twelfth node was healthy. One leaf at the thirteenth node was silvery-yellow from the base to the apex of the lamina, but on one side of the mid-rib the lamina was green and healthy. Numerous oospores occurred in the discoloured part. The other leaf at this node was completely silvery-yellow and contained young oospores in large numbers.

Both the leaves at the five nodes 14–18 were thickly infested with hyphae, oogonia, and oospores and particularly round the edges of the lamina where the silvering was more pronounced. A small inflorescence at the fourteenth node was found to contain in the main axis, hyphae with typical haustoria and oospores. The latter were also found in the perianth lobes round the ovary.

The plentiful occurrence of hyphae in the main stem having been established, this was next cut off immediately below the fourth node which was 10 cm. from ground level. Sections were cut through this node and hyphae were found. It could be seen easily with the naked eye that the pith of the main stem was brown. A median longitudinal section was cut through the node to include both the petioles* and no hyphae were found passing into the petiole of the one healthy leaf, nor into the lateral shoot in its axil. On the other side hyphae were found starting from the shrivelled and pinched-off stump of the petiole and extending into the main stem where they joined the general mass in the pith. The hyphae were not densely granular but appeared to be empty with only small scattered oil globules here and there. Haustoria were numerous. The upward course of the mycelium was next followed and it was found that the brown colour of the pith was visible from the fourth node as far as, and including, the seventh. Hyphae were found in the internodes and were present also in all the other internodes above, though here the pith was not discoloured.

As regards the leaves situated above the node already investigated, at the fifth node there was a leaf, opposite the one

* The base of the petiole of the inoculated leaf which had been removed on October 25th still remained.

inoculated, having a brown tinge on the exterior of the petiole. The lamina was beginning to shrivel at the extreme base near to the petiole and it appeared that the fungus was just about to enter it. Hyphae and oospores (the latter in great numbers) were found in the affected parts. At the sixth node, one leaf was withered and numerous oospores were present in the lamina and in the brown and withered petiole. The other leaf, judging by the presence of a light-coloured area on the lamina, was being invaded by the fungus. The petiole showed faint brown marks externally and hyphae and oospores were found in this and in the lamina. At both the seventh and eighth nodes, one of each pair of leaves was healthy and green and the other showed a light-coloured area close to the base of the lamina. The petioles of the invaded leaves were streaked with brown on the outside. The pairs of leaves at the ninth, tenth and eleventh nodes were all healthy and of good colour. Mention has already been made of the one leaf at the twelfth node which was green and healthy in contrast to its counterpart on the other side of the node which was silvery yellow.

All parts of the plant above the lowest place of inoculation (node 4) having been found infected, the base was next examined. Sections cut through the fourth node, already described, had revealed hyphae in the pith of the main stem. In addition to those traced upwards, there were some which extended to the extreme base of the sections (*i.e.* the lowest part of the node) and their presence there suggested that a downward penetration must also have taken place. The internode (3–4) was split longitudinally and it was found that the pith was brown and contained mycelium. At the third node one leaf was withered and its petiole was shrivelled as far as 5 mm. from the base (*i.e.* from the lamina downwards) but it contained no fungus to account for the injury. The other leaf and two lateral shoots at this node were healthy. Longitudinal sections of the node itself showed that the pith was crowded with hyphae and haustoria, and it was remarkable that neither the lateral shoots nor the two petioles were invaded.

The pith of the next internode (2–3) was brown and contained hyphae. At the second node, one leaf was withered and the other healthy; both the axillary shoots were withered. Oospores and hyphae were found in the lamina and petiole of the one leaf and in its axillary shoot. As regards the other leaf, which was normal, sections of the node showed that there was no invasion of this petiole but that the lateral shoot in its axil was thickly infested. The mycelium was present in the pith of the next internode (1–2) and this again was indicated by the brown colour. At the first node there was one normal leaf; the other

was missing, but the petiole remained. There were two long lateral shoots (9 cm.) which were healthy. Sections of the node showed that the pith contained mycelium but the axillary shoots and the petioles subtending them contained none. At this node the hyphae were of somewhat different appearance from that of hyphae seen in the higher parts of the host plant. They were even less granular and more transparent—a feature which was thought to indicate reduced vigour. All the sections had been treated with alkaline Azo Blue and the hyphae present in the first node showed a further difference in that they took up the stain less readily. The haustoria, however, were rapidly stained. In the internode 0–1, the hyphae were found extending nearly to node 0 which was below the level of the soil. Two lateral shoots from this node were healthy. No mycelium was found in the hypocotyl, nor in the roots.

From this examination it would appear that the conidia had germinated and had infected the plant within eight days without production of conidiophores. The fungus was able to form oospores in the petioles of the infected leaves and to pass on into the pith of the main stem. Here, presumably, it had grown both upwards and downwards (though faster and further in the former direction) until, near the apex of the plant, it had invaded and caused the discoloration of the leaves. It is remarkable that (as we have observed also in the Downy Mildew of the Hop), one leaf or lateral at a node may escape attack while the other becomes invaded, and while this may be explained on the assumption that the hyphae are sometimes by chance present on only one side of the main stem, it is more difficult to explain why, as at node 2, a lateral shoot should be invaded and the subtending leaf petiole remain free when the points of attachment of both to the main stem are in the same vertical line and extremely close together.

The silvery-yellow coloration of the uppermost leaves appears to be the most constant macroscopic feature of the disease. The large light-coloured areas or streaks which are to be seen on the leaves (not necessarily those near the apex of the stem) are less constant symptoms, and are apparently dependent on seasonal conditions. It seems probable that the main primary infection is brought about by the conidia produced on the yellow-coloured foliage at the top of the stems; these conidia presumably are carried to healthy leaves and under suitable weather conditions are able to infect and to form small angular spots bearing fresh conidiophores. Under some conditions, probably connected with the age of the host plant or with lack of humidity in the atmosphere, the fungus, often without fruiting on the surface of the lamina, spreads rapidly internally and

finding its lateral expansion limited by the veins, grows in a direction approximately parallel to them and thus finds its way into the petiole. A great many of the brightly-coloured areas seen on leaves under natural conditions extend to the base of the lamina at the place of junction with the petiole. It is probable that these large yellow-coloured streaks are indicative of an attempt at systemic infection rather than a result thereof*.

Summary.

1. *Peronospora Urticae*, founded by Berkeley in 1846 on *Botrytis Urticae* Libert MSS., has an oval conidium, minutely apiculate at the apex—as described by Berkeley and Broome. The present writers have previously pointed out that the conidium germinates by means of zoospores and that the species is therefore to be referred to the genus *Pseudoperonospora*.

2. In 1863 de Bary described a species having a broadly ovoid or subglobose conidium, very obtuse at the apex and with no apiculus and, misled through seeing a drawing sent by Berkeley to Caspary, identified it as *Peronospora Urticae* (Lib.). Subsequent authors (*e.g.* Berlese, Fischer, Migula, Gäumann) have followed de Bary in this identification.

3. The examples sent out under the name *Peronospora Urticae* in various Exsiccati are sometimes Berkeley's and sometimes de Bary's species.

4. The name *Peronospora deBaryi* nomen novum is proposed for de Bary's species.

5. *Pseudoperonospora Urticae* occurs on *Urtica dioica* and *U. urens*, and *Peronospora deBaryi* on *U. urens* only. The distribution of each species is given.

6. Living examples of *P. deBaryi* were first met with by the writers at Wye, Kent, in 1926; the study of these and the evidence obtained in an inoculation experiment have shown that *P. deBaryi* causes a systemic infection of the host-plant.

We wish to thank Mr J. Ramsbottom, of the British Museum (Natural History), London, and Miss E. M. Wakefield, of the Herbarium, Royal Botanic Gardens, Kew, for their helpful advice on numerous occasions.

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THE STRUCTURE AND MODE OF REPRODUCTION OF SIPHULA TABULARIS NYL.

By S. Garside, M.Sc., Bedford College, London.

(With Plate I and 4 Text-figures.)

There are some genera and species of lichens of which little or nothing is known about the spore-producing organs. In such, the systematic position cannot, as a rule, be determined with certainty, as the evidence indicating affinity must be derived entirely from the structure of the vegetative organs.

The genera *Thamnolia*, *Endocena* and *Siphula* have been included in the Usneaceae because of the structure of the vegetative thallus.

In *Thamnolia vermicularis* (Sw.) Ach., a widely distributed arctic and alpine lichen, pycnoconidia have been discovered, but apothecia are extremely rare, and the two descriptions of them which have been published differ in important respects.

In *Endocena* (one species, *E. informis* Cromb. in Patagonia) and *Siphula* (about fourteen species, widely distributed) the spore-producing organs are still unknown.

In all three genera, vegetative reproduction is probably the efficient means of dispersal, portions of the thallus becoming detached and distributed by the wind, on the feet of birds, or in other ways.

I have had an opportunity of studying in the field the three South African species of *Siphula* which occur frequently on the

Cape Peninsula and on the neighbouring mainland. In one of these, *Siphula tabularis* Nyl., there is a highly specialised mode of vegetative reproduction of a kind which has no parallel, as far as at present known, in any other genus of lichens.

Siphula tabularis Nyl. was first collected at the Cape by Thunberg, who obtained it from Table Mountain, between 1772 and 1779. After his return to Europe, Thunberg delayed publication of his lists and descriptions of Cape plants, and his list of Cape lichens appeared only in 1800 in the *Prodromus Plantarum Capensium.*

Long before this date, however, descriptions of *Siphula tabularis* were published, the first being in 1781, in the *Supplementum Plantarum* of Carl von Linné, as *Lichen verrucosus* Linn. fil. (p. 451).

Through the kindness of the late Dr B. Daydon Jackson, I examined the specimens of *Lichen verrucosus* in the Linnean Herbarium. The writing upon the herbarium sheet is that of the elder Linnaeus, and is *Lichen verrucosus* with the letter "T," which means Thunberg. There is also a small ticket with the number 519, probably in Thunberg's writing. There are two specimens, one about 10 cm., the other about 5 cm. in diameter. The letter "T" has been written under the smaller specimen.

The works of Acharius published between 1798 and 1814 contain brief descriptions of the plant: the first published figure appears in *Methodus Lichenum,* Tab. VII, fig. 3 as *Stereocaulon tabulare* Ach. Acharius noticed that the ends of certain branches are terminated by numerous wart-like granules; but he did not consider them as equivalent to fruit-bodies.

Nylander (*Synopsis Lichenum,* 1, p. 263, 1858) placed the plant in the genus *Siphula.* He thought that it might be a deformed condition of some other lichen.

It is unnecessary to cite subsequent references in detail, as they contain nothing of importance; there was no critical examination of the plant until a new collection was made at the Cape in 1857–58, by Dr Wawra, the material being placed in the hands of Massalongo (1) (1861), who gave the first detailed description accompanied by a large, but somewhat inaccurate coloured plate.

Massalongo states that the plant is always sterile. He describes the general habit, the ashy grey colour of the young horizontal thallus, with its brownish lower surface, and in older thalli the formation of upright podetia, the ends of which become constricted and produce numerous spherical bodies containing gonidia. He regards these structures as soredia. He compares the structure of the thallus of *Siphula ceratites* and "*Stereocaulon tabulare,*" as the lichen was called by Acharius,

and decides that the latter lichen must be placed in the genus *Siphula*.

A few additional collections of the lichen were made by Ecklon, Zeyher, Drège, Eaton, Wilms and MacOwan, but no detailed account has been published.

Habitat.

None of the earlier collectors mentions the curious habitat of *Siphula tabularis*.

The lichen occurs as large whitish or greyish patches upon the surface of sandstone rocks in the numerous small streams which drain the summit of Table Mountain and the mountain ranges of the Cape Peninsula and the adjoining mainland. Exact localities where collections have been made are cited at the conclusion of this account; the localities are almost all upon the Cape Peninsula, and more records from the mainland will be required before we can estimate the probable distribution of the lichen in South Africa as a whole.

In winter (April to September), the plant is frequently submerged for weeks; in summer, the streams dry up, and the plant is in a state of extreme desiccation. There is as yet no record of its occurrence in rivers where there is a constant water supply, and it does not thrive in the shade, though shade forms have been found. Almost all the localities recorded have been watercourses open to full sunlight. No doubt this preference for a seasonally fluctuating water supply and intense insolation restricts the distribution to comparatively high altitudes; on the lower slopes, the streamside vegetation will shade the watercourse to a considerable extent.

Most of the material studied was collected at altitudes of from 2000 to 3000 ft., the rarity of the plant at much lower (150 ft.) or much higher altitudes (above 3000 ft.) is probably correlated with the absence of a suitable environment at these altitudes.

The structure of the horizontal thallus.

The primary, or horizontal thallus (Pl. I, fig. 1) forms irregular patches up to 10 cm., in diameter, ashy grey above, reddish-brown or yellowish below. It is attached to the rock surface by a few stout rhizines of a blackish colour, which are irregularly distributed over the lower surface (Pl. I, fig. 4). The rhizines are massive bundles of hyphae arising in the medulla, and passing outwards through the lower cortex. Their dark colour is due to the included fragments of rock, rather than to the colour of the constituent hyphae (Text-fig. 2). They force themselves into cracks in the rock surface, and they are no

doubt subjected to considerable strain when water is rushing over the thallus during the period of the winter rains. Their function is probably entirely that of attachment; hence their stout solid structure, reminiscent of the haptera of many seaweeds.

The horizontal thallus (Text-fig. 1) has a bifacial structure. Towards the upper surface there is a well-defined, compact, paraplectenchymatous cortex, situated beneath which is the

Fig. 1. Transverse section of a portion of the horizontal thallus, passing through two adjacent thallus lobes, which have united by their cortices. Gonidial zone shaded. × 25.

Fig. 2. Transverse section of a horizontal thallus, passing through a rhizine. × 25.

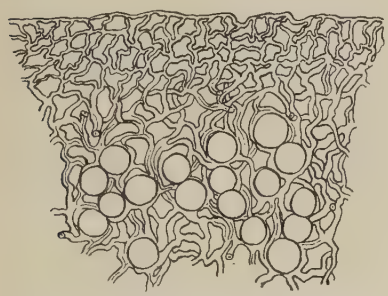


Fig. 3. Transverse section of thallus, showing cortex and portion of gonidial zone. × 620.

Fig. 4. Transverse section, hyphae of the medulla. × 620.

broad gonidial zone. The bright green algal cells are "chlorococcoid" but as the plants studied did not show actively dividing gonidia, their mode of division and reproduction was not determined.

The gonidia are from 7–10 μ in diameter, with an average diameter of 8 μ. They are surrounded by closely interwoven hyphae (Text-fig. 3), though penetration of gonidia by haustoria was not observed. Towards the centre of the thallus, the hyphae are more loosely arranged to form the medulla (Text-fig. 4),

and a considerable amount of air is normally included between the hyphae, and is exceedingly difficult to displace.

After soaking portions of the thallus in water for two days, the air remained, even though cut surfaces unprotected by cortex were in direct contact with the water. This property of the cortex may be of considerable importance, as it enables the lichen to retain an internal supply of gases during its period of submersion. It is, however, unusual to find an aerating system in plants of rapid streams, such plants (as *e.g.* in Podostemaceae) usually deriving their supply of the necessary gases from solution in water. However, as the cortex imbibes water freely, the gonidia may make use of gases which diffuse through it.

The lower surface of the thallus follows closely the irregularities of the substratum, and is bounded by a paraplectenchymatous cortex which is a little less well defined in its limits than the cortex of the upper surface. There is no gonidial zone towards the ventral surface.

Owing to repeated branching of the thallus in the horizontal plane, the branches are often closely crowded, and fusion may occur between the cortices of adjacent branches (Text-fig. 1), thus uniting most of these into a compact mass.

In favourable circumstances, when the thallus has attained a moderate size, the tips of the horizontal thallus-branches change their direction of growth, and become more or less vertical; this reaction however, does not occur in plants which have grown in deep shade, where the thallus continues its growth, but its branches remain of the horizontal type throughout and the special organs of reproduction about to be described are not readily formed.

Examples of the shade form of the thallus were found by Mr N. S. Pillans near Somerset West (Pillans, No. 4842). These were growing upon wet rocks in deep shade at the foot of a waterfall. The rocks would be wet by the spray from the waterfall for the greater part of the year, but never actually under water.

The thallus branches of these plants are elongated, much flattened, the lower surface yellowish, with a few massive rhizines. Probably the lichens had reached this unsuitable habitat owing to detached isidia derived from plants growing in full sunlight at a higher altitude, having been washed down by the stream.

Formation of Podetia and Isidia.

In a favourable habitat, one which receives full sunshine, growth takes a very different course. Even in quite young thalli, the tips of many of the thallus-branches assume a vertical

direction, forming short "podetia," as they may conveniently be termed (Pl. I, figs. 1 and 6). These vertical thallus-branches have a radial structure, a central medulla of loose hyphae being surrounded by a peripheral gonidial zone immediately below the cortex, which has the structure already described for the upper surface of the horizontal thallus.

A remarkable change now occurs at the flattened apex of each podetium. The end becomes verrucose, and small warts appear, from ten to fifty on each podetium. These verrucae enlarge considerably, and finally most of them become detached as minute spheres, each about 0·25 mm. in diameter. Each sphere leaves a small pit where it separates from the parent plant, the bottom of which is greenish, as the pit penetrates to the gonidial layer of the thallus. Each sphere, in section, is seen to consist of a mass of medullary hyphae with numerous groups of the normal gonidia, completely enclosed by a well-developed cortex of the type found in the thallus.

Thus these structures, which, like soredia, take their origin in the gonidial layer, have a more specialised structure than soredia. In being corticated, they approximate in structure to isidia, and here we shall consider them as such, though being of endogenous origin they differ from any isidium so far described.

The sequence of changes leading to the formation of isidia usually occurs at the apex of a podetium. Around a group of gonidia in the gonidial zone of this region, the hyphae become more compact and more closely interwoven, so as finally to produce in the gonidial layer a paraplectenchymatous cortex-like zone completely surrounding and enclosing the groups of gonidia. This new cortex is first differentiated on the side of the gonidial group towards the periphery of the podetium, and differentiation proceeds inwards until the gonidial group is completely enclosed (Pl. I, fig. 3 *a*). A number of groups of gonidia may become corticated in this way. Later, the cortex covering the end of the podetium is broken through by the enlarging isidia below it, which ultimately become detached, each leaving a small concavity marking the spot where it separated from the medulla (Pl. I, fig. 5 *a*).

As the isidia have their origin entirely within the gonidial zone, thus differing markedly from the usual exogenous production of isidia, it is suggested that the term *endisidia* might be applied to them.

After a number of isidia have been detached, the hyphae of the medulla are exposed directly at the end of the podetium, the normal gonidial layer having been more or less used up in the formation of isidia. Some gonidia may remain, and it is

probable that after further division of the algal cells, these gonidial groups may again form centres of origin of additional isidia.

There is every indication that, following the destruction of the cortex at the apex of a podetium, and the formation of isidia, further normal growth of the podetium ceases, though, as will be seen later, the length of a podetium can be increased by the germination of one or more gonidia *in situ*.

Germination of the Isidium.

There is a remarkable difference in the behaviour of the isidium according to the nature of the substratum upon which it germinates.

If the isidium falls upon a rock surface or upon the leaves of small aquatic mosses, in a situation favourable for germination, it attaches itself by means of short hyphae growing out from the cortex at its point of contact with the substratum. The isidium, at first spherical, rapidly enlarges, and when about 0·5 to 1 mm. in diameter, becomes dorsiventrally flattened. A gonidial zone is organised towards the upper, or illuminated surface, gonidia disappearing from the lower, attached surface (Pl. I, fig. 2 *a*). The young thallus thus organised is at first almost circular in outline, but its margin becomes lobed when it has attained a diameter of about 1·5 mm. (Pl. I, fig. 2 *b*), and later, when the young thallus is about 3 or 4 mm. in diameter, the tips of some of the thallus-lobes may leave the substratum, and take on a vertical direction of growth, to form podetia (Pl. I, fig. 2 *c*). Germination of isidia upon rocks occurs at the beginning of the dry season, when the stream bed is still wet enough to afford sufficient moisture. Obviously, isidia detached when the stream is in flood may be carried away to a considerable distance, thus affording a means of distribution of the plant, but in a downstream direction only.

An isidium, or group of isidia may, however, germinate *in situ*. Here, the isidium grows out at once to form a thallus of radial structure, which is essentially a continuation of the parent podetium. The tip of the new cylindrical thallus again forms isidia, and if germination *in situ* is repeated, a long thallus-branch may be built up, each segment of which is the product of an isidium (Pl. I, fig. 7). Frequently, branches of six or seven segments are produced, the extent of the thallus formed by each isidium being marked by constrictions.

A very remarkable feature of this method of thallus formation is that the growth of one isidium more or less completely inhibits the growth of the remaining isidia which have been formed at the apex of the podetium. It is rare to find two or three isidia germinating at the end of a podetium (Pl. I, fig. 7 *a*).

Finally, if an isidium which has become completely detached from the podetium falls upon the cortex of the parent plant, or upon that of a neighbouring plant, it attaches itself, and grows to form a thallus of radial structure (Pl. I, fig. 7 *b*).

Thus, when germination takes place upon a foreign substra tum (rock, moss etc.) a dorsiventral thallus is formed; when upon the *Siphula* thallus, the young plant has a radial structure from the first. When thallus-branches (whatever their origin) come into contact, they tend to become firmly united by intermingling hyphae from the cortices at the point of contact. In this way, the branches of a thallus are firmly held together to form fruticose coral-like masses, and rigidity is thus ensured to old plants in which considerable branching has occurred.

Function of the Isidia.

The function of isidia in the biology of lichens has given rise to considerable discussion.

The older view is that they are organs of vegetative reproduction, minute but complete lichen thalli, carrying the necessary gonidia, and endowed with the power of germination upon suitable substrata. Many lichens are known, however, in which the isidia are not readily detached.

More recently it has been contended that their main function is to increase the assimilating surface of the thallus. Thus Darbishire has shown for *Peltigera praetextata* Zopf (2) that the isidia have the structure of small dorsiventral thalli attached to the parent.

A third explanation is that they are somewhat abnormal growths, appearing as the result of damage to the cortex of the parent plants, and though this explanation may be true for some lichens, it obviously does not cover those where we have parallel forms or strains, one more or less isidiose under almost all conditions of environment, the other entirely lacking the power to produce isidia (Du Rietz (3)). Probably no one explanation will cover all cases.

In *Siphula*, although the isidia differ from typical isidia in being endogenous, they combine very effectively both the functions of vegetative reproduction and increase of the assimilatory surface of the parent thallus; the first if they become detached and germinate on foreign substratum, the second if they germinate *in situ*, or upon the cortex of the parent.

Mode of distribution of Isidia.

As far as is known at present, the isidia constitute the only method of reproduction of *Siphula tabularis*. They are comparatively large bodies, visible to the naked eye, and probably

much too large to be carried long distances by the wind. As already indicated, the curious habitat (in watercourses) will provide for their distribution in a downstream direction; the problem being the ascent of the plant to the fairly high altitudes sometimes reached.

Mr Pillans, who has examined a large number of habitats suggests the following possibilities.

Very strong winds may, in the dry season, carry isidia to slightly higher altitudes, thus gradually colonising the upper parts of the stream bed. In the summer, cattle frequently follow a watercourse when feeding, as in the dry season more succulent herbage is to be found on the stream bank than on the open hillside. This habit was no doubt followed by the many species of antelope formerly found in the Cape Peninsula. Finally, birds are attracted to the watercourses in the summer, and may carry the isidia attached to their feet, in the manner known to occur with some seeds, a method which would account for distribution over a wide area.

Records.

The material studied has been obtained from the following localities, all on rocks in stream beds:

Cape Peninsula.

Farmer Peck's Valley, Muizenberg. February 14th, 1920. 760 ft. Garside.

Summit of Table Mountain. May 31st, 1922. Pillans, 4211.

Saddle between Devil's Peak and Table Mountain. 2850 ft. Pillans, 3252.

Head of Kasteel's Poort, Table Mountain. 2450 ft. Pillans, 3550.

Between Wynberg upper reservoir and Disa Gorge. 2420 ft. Pillans, 3969.

Middle part of Silvermine Valley. 500 ft. Pillans, 3831.

Plateau on the Muizenberg. 900 ft. Pillans, 3168.

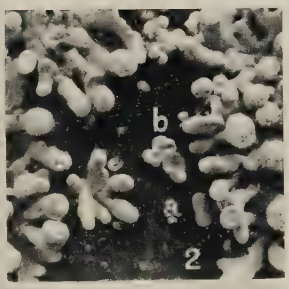
West of Paul's Berg, South West Coast. 150 ft. Pillans.

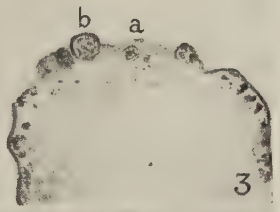
Abundant on north side of summit of Noord Hoek Mountain, near a small spring. January 1922. Pillans.

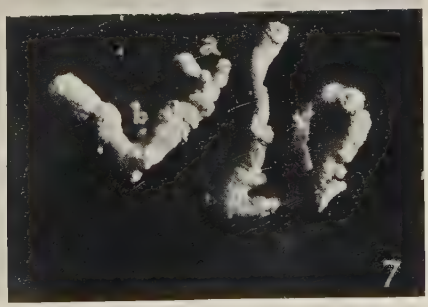
Mainland.

Rare on moist shaded rock in ravine off Staircase Ravine, Diep Gat Kloof, above Somerset West, Cape Province. April, 1925. Pillans, 4842.

On rocks, waterfall on the Swartberg near Swellendam. March, 1887. P. MacOwan.







SIPHULA TABULARIS NYL.

Bushman's Country, Cape of Good Hope. "On the ground." Zeyher.

Cape of Good Hope, Drège. Ex. Herb. Hampe. 1877.

Tulbagh Waterfall. Garside.

EXPLANATION OF PLATE I.

Siphula tabularis Nyl.

Fig. 1. Horizontal thallus growing upon sandstone rock, Farmer Peck's Valley, Muizenberg. The numerous pits at the ends of the vertical podetia are points at which isidia have been detached. Between the older plants, isidia are germinating upon the rock surface. × 2·5.

Fig. 2. A small portion of Fig. 1, showing successive stages (*a*, *b* and *c*) in the germination of isidia. × 2·5.

Fig. 3. Longitudinal section through the apex of a podetium, with developing isidia. At *a*, a cortex is forming around a gonidial group; *b*, section of an almost mature isidium. × 50.

Fig. 4. Lower surface of a small thallus, showing massive blackish rhizines. × 3. Pillans, 4211.

Fig. 5. Longitudinal section through the apex of a podetium, showing three isidia about to be liberated. At *a*, two isidia have been detached, leaving concave pits in the medulla. × 50.

Fig. 6. Small portion of a horizontal thallus, showing podetia with groups of spherical isidia at their apices. × 3. Pillans, 4211.

Fig. 7. Isidia germinating *in situ* at the ends of podetia. At *a*, three isidia from the terminal groups are germinating, forming three thalli of radial structure. At *b*, an isidium has become attached to the cortex of the old plant, and is enlarging to form a radial thallus. × 3.

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THE INVESTIGATION OF ASPERGILLI BY SEROLOGICAL METHODS.

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An extensive literature has accumulated about the serological differentiation of pathogenic bacteria, particularly animal pathogenic bacteria, but references to serological studies on pathogenic and saprophytic fungi are extremely limited. In the present paper I do not propose to discuss all the literature on this subject, but will review some of the references which seem to be more closely connected with the present investigation.

Malvoz (1901) made some serological studies on a certain

Saccharomyces (la levure du vin de Huy) and found that the immune serum secured from the rabbit inoculated with 2 c.c. emulsion of the yeast spores gave an agglutinating reaction at concentrations ranging from 1 : 30 to 1 : 40, while normal serum agglutinated very slightly at the dilution of 1 : 1. However, in his conclusion he made the following statement: "Des diverses propriétés susceptibles d'être acquises par un sérum d'animal immunisé, on ne constate in vitro dans le sang frais des animaux traités par les blastomycètes que le pouvoir agglutinant, et à un titre peu élevé, malgré la répétition des injections. Le pouvoir cytotoxique du sérum n'apparaît pas in vitro, soit à cause de l'absence d'anticorps sensibilisateur dans les humeurs, soit parce que la capsule des levures les protège contre les alexines."

Schütze (1903), also working with certain yeasts, concluded that he could hardly find any differentiation between his "Getreide-" and "Kartoffelhefe" by means of agglutination.

Citron (1905), in his studies on Favus and Trichophyton fungi, stated that the agglutination tests were not satisfactory owing to the technical difficulty in obtaining homogeneous emulsions, but precipitation tests gave some distinctive reactions. The immune sera precipitated the homologous strains more extensively than the heterologous ones, nevertheless, these differences might not be sufficient to classify them as distinct species.

Schütze (1911) further tried to differentiate between his yeasts by complement fixation. He found it impossible to distinguish cereal- from potato-yeasts by this method, but considered it possible to differentiate "Ober-" and "Untergärige Bierhefe," and further to distinguish these from cereal- and potato-yeasts.

Blakeslee (1915), working with *Mucor* sp. (according to him the species appears closely allied to *M. hiemalis*), noticed that repeated intravenous injection of rabbits with the fungus spores failed to cause the development in their blood of cytolytic substances capable of dissolving such spores, and he was also unsuccessful in showing any specific sexual reaction such as had been suggested in precipitin tests (1913) with the "press-saft" from the mycelium of this same mould, but the inoculations might apparently stimulate the formation of antibodies that caused them to agglutinate in such a way as stated below. According to him the immune sera caused a distinct clumping of both male and female spores in dilutions up to 1 : 1200, producing an irregular roughening of the edges of the spore mass at the bottom of the tubes. A similar clumping of spores was found in the control serum, but only at the tested dilutions of 1 : 30, 1 : 150 and 1 : 300. The immune sera were also tested with spores of two other moulds—*Absidia glauca* and a species of the *Mucor racemosus* type. There seemed to be slight agglu-

tination with both species. To explain this result he suggested: "It is possible that the rabbits tested had received so many spore injections that their sera had largely lost their specificity and so reacted with spores of any species of this mould group."

Serological studies on *Aspergillus* have been very few, so far as I am aware. The only available paper on this subject is the study of *Aspergillus fumigatoides* by Sartory (1922), who made some serological studies to distinguish *Aspergillus fumigatoides* from *A. fumigatus*. He stated briefly that the immune serum obtained from the rabbit inoculated with the spores of *A. fumigatoides* could agglutinate the spores of this species at the dilution of 1 : 50, but it was unable to agglutinate the spores of *A. fumigatus*. No details, however, are supplied.

From a consideration of the meagre literature it appears questionable whether serological reactions can serve as important tests for separating various species and groups of fungi. It would seem advisable to study more extensively a larger number of the strains and species of fungi morphologically as well as biologically, and to learn more of the relation existing between their serological affinities and other characteristics.

The following experiments were performed while I was working in the Lister Institute, London. The study is by no means complete, but it seems desirable to publish a first report. It is proposed to resume the study shortly after my return to Japan, and further reports will be made.

Selection of cultures.

The cultures selected for the study were mostly obtained from the National Collection of Type Cultures, Lister Institute, London. The morphology of the fungi was carefully studied and they were arranged according to their morphological relationships. This arrangement agrees with that of Thom and Church (1926) in the most important points. Cultural information given in the following list is obtained from growth upon Czapek's agar kept at 25° C. for a week. The reference number of the National Collection is printed in brackets.

I. *Group A.*

Colonies green or greenish when conidia formed; stalks smooth (compare Group *D*), septate; sterigmata usually in one series (compare Group *E*).

1. *Aspergillus Amstelodami* (1945, isolated by Miss M. B. Church, Washington, D.C., U.S.A.).
2. *Aspergillus glaucus*, No. 1 (1830).
3. *Aspergillus glaucus*, No. 2 (isolated from tobacco of cigarettes by H. W. Wollenweber, Dahlem, Berlin).
4. *Aspergillus herbariorum* (1216).

II. *Group B.*

Colonies black to dark brown when conidia formed (compare other groups); stalks smooth; sterigmata mostly in two series; conidia rough or spinulose.

5. *Aspergillus niger*, A, No. 1 (603)
6. *Aspergillus niger*, A, No. 2 (1161)
7. *Aspergillus niger*, A, No. 3 (799)

} Liquefying gelatin.

8. *Aspergillus niger*, B, No. 1 (308)
9. *Aspergillus niger*, B, No. 2 (1692)
10. *Aspergillus niger*, B, No. 3 (594)

} Not liquefying gelatin.

11. *Aspergillus carbonarius* (1325, isolated by Thom and Church).
12. *Aspergillus awamori* (2044).
13. *Aspergillus luchuensis* (1017, isolated by Hanzawa, Japan).
14. *Aspergillus pulverulentus* (1324, isolated by Thom and Church).

III. *Group C.*

Colonies dark green when conidia formed, becoming greenish black with age; vesicles also green; sterigmata in one series (compare Group *E*), almost parallel to axis of the stalk, arising mostly on the upper half of the vesicle (compare other groups).

15. *Aspergillus fumigatus*, No. 1 (1373).
16. *Aspergillus fumigatus*, No. 2 (982).

IV. *Group D.*

Colonies mostly some shade of green or yellow-green or greenish yellow; stalks mostly septate, finely pitted (compare Groups *A*, *C* and *E*); sterigmata in one series (compare Groups *E* and *F*).

17. *Aspergillus Oryzae* (598).
18. *Aspergillus parasiticus* (975, isolated by Speare, Honolulu).

V. *Group E.*

Colonies yellowish green to pea-green; stalks predominantly septate, smooth, occasionally warted but never pitted (compare Groups *D* and *F*); sterigmata in two series (compare Groups *A*, *C* and *D*).

19. *Aspergillus nidulans* (793).
20. *Aspergillus versicolor* (1883, isolated by H. R. Jones, Bristol University).
21. *Aspergillus Sydowii* (1944, isolated by N. Kopeloff, Louisiana, U.S.A.).

VI. *Group F.*

Colonies orange-yellow to ochraceous, but never green (compare other groups); stalks non-septate, occasionally septate,

pitted (compare Group *E*); sterigmata usually in two series (compare Group *D*).

22. *Aspergillus ochraceus* (979, isolated by Thom and Church).
23. *Aspergillus Tamarii* (599, obtained from Thom and Church).

VII. *Group G.*

Species other than *Aspergilli.*

24. *Pencillium glaucum* (isolated from apple fruit-rot by H. W. Wollenweber, Dahlem, Berlin).
25. *Gloeosporium fructigenum* (Do.).

Method of Immunisation.

Rabbits were inoculated with increasing doses of the spore suspensions of the following six species of *Aspergillus*: (1) *Aspergillus Amstelodami*; (2) *A. glaucus*, No. 1; (3) *A. niger*, A, No. 1; (4) *A. niger*, B, No. 1; (5) *A. carbonarius*; (6) *A. fumigatus*, No. 1. The fungi were planted on ordinary agar slants and kept at 25° C. for a week. The spores were collected in sterilised physiological saline by scraping off with a platinum needle. These

Table I. *Approximate number of spores used for inoculation.*

No. of inoculation	*Amstelodami*	*glaucus*, No. 1	*niger*, A, No. 1	*niger*, B, No. 1	*carbonarius*	*fumigatus*, No. 1
1	32,000,000 in 1 c.c.	12,000,000 in 1 c.c.	40,000,000 in 1 c.c.	36,000,000 in 1 c.c.	10,000,000 in 1 c.c.	35,000,000 in 1 c.c.
2	64,000,000 in 2 c.c.	24,000,000 in 2 c.c.	80,000,000 in 2 c.c.	72,000,000 in 2 c.c.	20,000,000 in 2 c.c.	70,000,000 in 2 c.c.
3	22,000,000 in 0·5 c.c.	12,000,000 in 0·5 c.c.	20,000,000 in 0·5 c.c.	15,000,000 in 0·5 c.c.	4,000,000 in 0·5 c.c.	20,000,000 in 0·5 c.c.
4	32,000,000 in 1 c.c.	15,000,000 in 1 c.c.	30,000,000 in 1 c.c.	25,000,000 in 1 c.c.	5,000,000 in 1 c.c.	30,000,000 in 1 c.c.
5	35,000,000 in 2 c.c.	30,000,000 in 2 c.c.	70,000,000 in 2 c.c.	50,000,000 in 2 c.c.	10,000,000 in 2 c.c.	35,000,000 in 2 c.c.
6	35,000,000 in 2 c.c.	30,000,000 in 2 c.c.	80,000,000 in 2 c.c.	70,000,000 in 2 c.c.	15,000,000 in 2 c.c.	35,000,000 in 2 c.c.
7	65,000,000 in 2 c.c.	50,000,000 in 2 c.c.	150,000,000 in 2 c.c.	100,000,000 in 2 c.c.	25,000,000 in 2 c.c.	70,000,000 in 2 c.c.
8	65,000,000 in 2 c.c.	60,000,000 in 2 c.c.	150,000,000 in 2 c.c.	100,000,000 in 2 c.c.	25,000,000 in 2 c.c.	100,000,000 in 2 c.c.
9	65,000,000 in 2 c.c.	60,000,000 in 2 c.c.	150,000,000 in 2 c.c.	100,000,000 in 2 c.c.	25,000,000 in 2 c.c.	—
10	65,000,000 in 2 c.c.	60,000,000 in 2 c.c.	150,000,000 in 2 c.c.	100,000,000 in 2 c.c.	25,000,000 in 2 c.c.	—

spore suspensions were centrifugalised and supernatant fluids were discarded and replaced with sterilised saline. The tubes containing the spore suspensions were left on the test-tube stand until the larger number of the clumps settled in the bottom of the tubes, and the supernatant homologous spore

suspensions were collected in separate tubes. The suspensions were heated for forty-five minutes at 65° C. The inoculations were made at intervals of six days. The first two injections were given subcutaneously and the subsequent eight inoculations were made intravenously. The number of spores inoculated was counted by means of Thoma's counting chamber. An approximate number of the spores used for inoculation is shown in Table I.

All the rabbits were bled from the marginal ear vein on the ninth day after the last inoculation. Sera were separated by pipetting from the clot after coagulation. They were always kept in a cold room, as the addition of any preservative was not advisable.

Agglutination Tests.

An extensive series of agglutination tests with homologous antigens as well as with heterologous antigens was performed, but owing to technical difficulties in securing good spore emulsions, the results were not satisfactory. A large number of the spores suspended in normal sera settled within thirty to sixty minutes and formed a uniform layer on the bottom of the tubes in the same manner as in the immune sera, therefore no accurate reading of agglutinating titre could be made. In testing anti-*Amstelodami* serum against homologous antigens, however, I found a slight but distinct clumping of spores at dilutions up to 1 : 80 after incubation for one hour at 57° C., whereas in the normal serum much slighter clumping was observed but only at dilutions of 1 : 20 and 1 : 40. Nevertheless, any cross tests proved to be unsatisfactory, since the reading was unreliable with such low titres.

Further, in connection with these agglutination tests, two more rabbits were inoculated with spore suspensions of *Aspergillus Amstelodami* prepared in the two following ways: (1) The suspension was heated in the same manner as described above, and then centrifugalised. The spores were separated from the supernatant fluid, and dried at 37° C. After thorough drying they were ground in a mortar and again emulsified by addition of the fluid which had been separated. (2) The spore suspension was boiled for twenty minutes instead of being heated at 65° C. for forty-five minutes. The method of inoculation was the same in all essential respects. In tests of the immune serum prepared by the first method no striking increase of titre was noticed, and in the second there appeared no noticeable difference between the immune and the normal serum.

From these results it may be inferred that agglutination methods have not proved satisfactory in classifying or differentiating the fungi.

Precipitation Tests.

The precipitation tests were more satisfactory. An extensive series was carried out by using filtrates of the cultures (ordinary broth) which had been incubated at 25° C. for seven weeks. Clear filtrates were easily secured by passing the cultures through filter paper. They were neutralised with KOH, if the filtrates were very acid. The filtrates were diluted with saline in the proportion of 1 : 1. The first reading was made after an incubation period of one hour at 37° C., and the final reading was made after keeping the tubes in the cold room overnight. For controls saline and normal sera at various dilutions were used. The results of the experiments are shown in the following tables (Tables II–VII).

Table II. *Precipitation test with anti-*Amstelodami *serum.*

	Immune serum				Normal serum			
Antigens	1 : 10	1 : 20	1 : 40	1 : 80	1 : 10	1 : 20	1 : 40	Saline
Amstelodami	++	+	+	±	−	−	−	−
glaucus, No. 1	++	+	±	−	−	−	−	−
herbariorum	+	+	±	−	−	−	−	−
niger, A, No. 1	++	±	−	−	+	−	−	−
niger, B, No. 1	++	±	−	−	+	±	−	−
awamori	++	±	−	−	±	−	−	−
carbonarius	+	±	−	−	−	−	−	−
luchuensis	+	±	−	−	±	−	−	−
pulverulentus	++	+	−	−	±	−	−	−
fumigatus, No. 1	±	−	−	−	−	−	−	−
Oryzae	+	+	−	−	−	−	−	−
parasiticus	+	±	−	−	−	−	−	−
nidulans	+	±	−	−	−	−	−	−
versicolor	+	±	−	−	−	−	−	−
Sydowii	+	±	−	−	−	−	−	−
ochraceus	±	−	−	−	−	−	−	−
Tamarii	+	±	−	−	−	−	−	−

+ denotes distinct positive reaction, number of this sign shows the degree of the reaction; ± denotes trace; − denotes negative reaction.

As shown by Table II precipitation took place most extensively when anti-*Amstelodami* serum was tested with the homologous antigen. The serum also showed a certain degree of group specificity common to members of this group. *A. fumigatus*, No. 1, appears to be similar in the serological behaviour to *A. ochraceus*, but this reaction cannot serve as an important test for classifying these fungi, since there is no such close similarity in morphological characters. In connection with this experiment attention must be paid to the fact that there was always some slight precipitation when normal sera were added to filtrates of cultures of *Aspergillus niger* at dilutions of 1 : 10

or 1 : 20, and also with filtrates of *A. awamori*, *A. luchuensis* and *A. pulverulentus* at dilution of 1 : 10. No interpretation of the cause of this reaction can be properly made at this moment, as all the filtrates were practically neutral and moreover no such precipitation was observed in the remaining filtrates. It is suggested, however, that there might be some correlation between this reaction and other characteristics common to the members of Group *B*, because all these fungi are classified under this group. As a whole, this immune serum appeared to be more or less reactive to all *Aspergilli* studied. In this respect this immune serum cannot be considered so highly specific as other sera possessing much lower titre.

Table III. *Precipitation test with anti-*glaucus *serum.*

	Immune serum				Normal serum			
Antigens	1 : 10	1 : 20	1 : 40	1 : 80	1 : 10	1 : 20	1 : 40	Saline
glaucus, No. 1	++	++	+	±	−	−	−	−
glaucus, No. 2	++	+	+	−	−	−	−	−
Amstelodami	±	−	−	−	−	−	−	−
herbariorum	±	−	−	−	−	−	−	−
niger, A, No. 1	+	±	−	−	+	−	−	−
niger, B, No. 1	+	±	−	−	+	±	−	−
carbonarius	−	−	−	−	−	−	−	−
awamori	+	±	−	−	±	−	−	−
luchuensis	±	−	−	−	±	−	−	−
pulverulentus	+	±	−	−	±	−	−	−
fumigatus, No. 1	−	−	−	−	−	−	−	−
Oryzae	−	−	−	−	−	−	−	−
parasiticus	−	−	−	−	−	−	−	−
nidulans	−	−	−	−	−	−	−	−
versicolor	±	−	−	−	−	−	−	−
Sydowii	−	−	−	−	−	−	−	−
ochraceus	−	−	−	−	−	−	−	−
Tamarii	−	−	−	−	−	−	−	−

See footnote to Table II.

The titre of the anti-*glaucus* serum was rather low as compared with the previous one, but the reaction appeared to be more specific, since, as shown by Table III, there was practically no noticeable reaction even with the related species, such as *A. Amstelodami* and *A. herbariorum*. Some precipitation was noticed when the antiserum was tested with antigens belonging to Group *B*. As has been already stated, this reaction might be largely non-specific. *Aspergillus versicolor* showed some relation in the precipitation test to *A. Amstelodami* and *herbariorum*, but this reaction appeared to have no significance for classification, since no apparent relation could be found in morphological characteristics between this particular species and any of Group *A*.

Table IV. *Precipitation test with anti-*fumigatus *serum.*

Antigens	Immune serum 1:10	1:20	1:40	1:80	Normal serum 1:10	1:20	1:40	Saline
fumigatus, No. 1	+	+	−	−	−	−	−	−
fumigatus, No. 2	+	±	−	−	−	−	−	−
niger, A, No. 1	+	±	−	−	+	−	−	−
niger, B, No. 1	+	±	−	−	+	±	−	−
carbonarius	−	−	−	−	−	−	−	−
Amstelodami	−	−	−	−	−	−	−	−
glaucus	−	−	−	−	−	−	−	−

See footnote to Table II.

Unfortunately the rabbit inoculated with the spores of *A. fumigatus* died shortly after the eighth inoculation, consequently the experiment was made only with the serum removed after the sixth inoculation. Owing to the lack of data no decisive conclusion can be drawn from this experiment, but so far as the present experiment is concerned, this antiserum appears to have a precipitin which is specific for strains of *A. fumigatus*.

Table V. *Precipitation test with anti-*niger, *A, No.* 1, *serum.*

Antigens	Immune serum 1:10	1:20	1:40	1:80	Normal serum 1:10	1:20	1:40	Saline
niger, A, No. 1	+++	++	+	±	+	−	−	−
niger, A, No. 2	+++	++	+	±	+	−	−	−
niger, B, No. 1	+++	++	+	±	+	±	−	−
carbonarius	++	+	±	−	−	−	−	−
awamori	++	+	±	−	±	−	−	−
luchuensis	++	+	±	−	±	−	−	−
pulverulentus	++	+	±	−	±	−	−	−
Amstelodami	+	+	−	−	−	−	−	−
glaucus, No. 1	++	+	−	−	−	−	−	−
herbariorum	+	−	−	−	−	−	−	−
fumigatus, No. 1	++	±	−	−	−	−	−	−
Oryzae	+	−	−	−	−	−	−	−
parasiticus	±	−	−	−	−	−	−	−
nidulans	+	−	−	−	−	−	−	−
versicolor	±	−	−	−	−	−	−	−
Sydowii	±	−	−	−	−	−	−	−
ochraceus	±	−	−	−	−	−	−	−
Tamarii	±	−	−	−	−	−	−	−

See footnote to Table II.

As shown by Table V the anti-*niger*, A, No. 1 serum can be used to identify the homologous strains, and at the same time to differentiate the members of this group as a whole, if the titre is taken into consideration. In testing the antiserum with some filtrates of cultures of *A. niger* there was practically no noteworthy difference in precipitation reactions between any of these strains, whereas by biochemical tests we could find at least two distinct types, viz. one liquefying gelatin and the

other not liquefying it. Therefore, all the strains of *Aspergillus niger* are considered to be identical from the precipitation standpoint. This immune serum is also more or less reactive with any species of *Aspergillus*.

Table VI. *Precipitation test with anti-*niger, *B, No.* 1 *serum.*

	Immune serum				Normal serum			
Antigens	1 : 10	1 : 20	1 : 40	1 : 80	1 : 10	1 : 20	1 : 40	Saline
niger, B, No. 1	++	±	−	−	+	±	−	−
niger, B, No. 2	++	±	−	−	+	−	−	−
niger, A, No. 1	+	±	−	−	+	−	−	−
carbonarius	−	−	−	−	−	−	−	−
awamori	±	−	−	−	±	−	−	−
luchuensis	±	−	−	−	±	−	−	−
pulverulentus	±	−	−	−	±	−	−	−
fumigatus, No. 1	−	−	−	−	−	−	−	−
Amstelodami	−	−	−	−	−	−	−	−
glaucus, No. 1	−	−	−	−	−	−	−	−
herbariorum	−	−	−	−	−	−	−	−
Oryzae	−	−	−	−	−	−	−	−
parasiticus	−	−	−	−	−	−	−	−
nidulans	−	−	−	−	−	−	−	−
versicolor	−	−	−	−	−	−	−	−
Sydowii	−	−	−	−	−	−	−	−
ochraceus	−	−	−	−	−	−	−	−
Tamarii	−	−	−	−	−	−	−	−

See footnote to Table II.

The titre of the anti-*niger*, B, No. 1 serum was very low as compared with the foregoing one. In all probability this might be due to the individuality of the rabbit inoculated, and not to the characteristics of the strain. On this point, however, further investigation is necessary.

Table VII. *Precipitation test with anti-*carbonarius *serum.*

	Immune serum				Normal serum			
Antigens	1 : 10	1 : 20	1 : 40	1 : 80	1 : 10	1 : 20	1 : 40	Saline
carbonarius	++	+	±	−	−	−	−	−
niger, A, No. 1	++	±	−	−	+	−	−	−
niger, B, No. 1	++	+	−	−	+	±	−	−
awamori	+	−	−	−	±	−	−	−
luchuensis	+	−	−	−	±	−	−	−
pulverulentus	+	−	−	−	±	−	−	−
Amstelodami	±	−	−	−	−	−	−	−
glaucus, No. 1	±	−	−	−	−	−	−	−
herbariorum	±	−	−	−	−	−	−	−
fumigatus, No. 1	+	−	−	−	−	−	−	−
Oryzae	+	−	−	−	−	−	−	−
parasiticus	−	−	−	−	−	−	−	−
nidulans	−	−	−	−	−	−	−	−
versicolor	−	−	−	−	−	−	−	−
Sydowii	−	−	−	−	−	−	−	−
ochraceus	−	−	−	−	−	−	−	−
Tamarii	−	−	−	−	−	−	−	−

See footnote to Table II.

Some precipitation occurred when the anti-*carbonarius* serum was tested with filtrates of cultures of *A. Amstelodami* and other related species. I do not think however that the result is of importance for the purpose of my present investigation, because, as shown in preceding tables, practically no specific reaction was noticed when the filtrate of *A. carbonarius* was tested with either of the two sera, viz. the anti-*Amstelodami* serum and the anti-*glaucus* serum, and moreover this species is not considered to be closely related to any of Group *A* in morphological relations.

It seemed advisable to repeat the precipitation tests by using some extracts prepared directly from the organisms. Accordingly the following methods of extraction were employed. Five grams of organisms, dried at 60° C., were thoroughly ground in a mortar. To the mass was added 100 c.c. absolute alcohol and extraction allowed to proceed for seven hours at boiling point in a reflux condenser. The extract was evaporated to get rid of the alcohol, and subsequently saline was added slowly. The solution was then passed through filter paper and finally through a Berkefeld filter*. Five grams of organisms, dried in the same manner as described above, were thoroughly ground in a mortar. To the mass was added 100 c.c. of 0·1 per cent. ethylene diamine solution. The solutions were put in an electric shaker for four hours, and then left on the laboratory bench overnight. The following morning the solutions were filtered through paper and finally through a Berkefeld filter†.

The results of the precipitation tests with these extracts proved unsatisfactory, no precipitations being noted. It is curious that no precipitation took place with these extracts, whereas with filtrates uniform success was obtained. This point will be discussed later.

From the results obtained in the foregoing experiments it may be concluded that precipitation tests are of some value in differentiating some strains or species of *Aspergillus*, but they cannot be used as the basis for classification inasmuch as no apparent relation can be found in some particular instances between serological affinities and morphological characteristics.

Complement Fixation Methods.

So far as my experiments have gone, complement fixation tests have proved by far the most promising for differentiating these fungi, since reactions are definitely observed in the higher dilutions of sera.

* Method employed by Eagles (1927).
† Method employed by Citron (1905).

The reaction of the reagents and glasswares has been found to have an important bearing on the accuracy of the test. Acidity and alkalinity may give rise to false reaction which may be positive or negative according to the degree of acidity or alkalinity. The technique employed was as follows:

For fixation: 0·5 c.c. of immune sera at various dilutions.
0·5 c.c. of antigens in saline (1 : 200).
0·5 c.c. of complement (1 : 10).

For haemolysis: 0·5 c.c. of amboceptor (daily titrated).
0·5 c.c. of sheep red cells in saline (1 : 20).

(i) Immune sera were inactivated by heating for half-an-hour at 56° C.

(ii) Antigens were prepared in the following manner. The fungi were planted on Czapek's agar and kept for one week at 25° C. The spores were collected in saline in the same manner as already described. To prevent the extraction from the media of substances that may render antigen non-specific they were washed at least twice with saline. This was performed by centrifugalising them and removing the supernatant fluids with a pipette. The spores were emulsified by addition of saline in the proportion of 1 c.c. of the spore mass to 200 c.c. of saline.

(iii) Freshly prepared complement of guinea-pigs was used in a ten per cent. dilution made with saline.

(iv) Erythrocytes from sheep were used after they had been washed several times and made up to a five per cent. suspension with saline.

(v) Amboceptor was obtained by successive inoculation of a rabbit with the above-mentioned sheep red cells. The serum was heated at 56° C. for thirty minutes on three successive days. The balance of the haemolytic system was obtained by means of an amboceptor titration in the same method as generally applied for the Wassermann test.

In the beginning of the work the fixation was accomplished by placing the test-tubes in the incubator at 37° C. for one hour, but later I found that more reliable and complete reactions were obtained when the fixation was extended overnight in the cold room (method of Lol, 1927). The following morning the sheep red cells and amboceptor were added and incubated at 37° C. for one hour. The first reading was made after the incubation period of one hour, but the final reading was made after keeping the tubes in the cold room overnight. For controls the following three tests were made: (i) saline instead of immune serum; (2) saline instead of antigen; (3) normal serum instead of immune serum.

Table VIII. *Complement fixation with anti-*Amstelodami *serum*

Antigens	Controls			Serum dilution						
	C. 1	*C.* 2	*C.* 3	1:20	1:40	1:80	1:160	1:320	1:640	1:1280
Amstelodami	++	++	++	−	−	−	−	−	⊥	±
glaucus, No. 1	++	++	++	−	−	−	⊥	±	++	++
glaucus, No. 2	++	++	++	−	−	−	⊥	±	++	++
herbariorum	++	++	++	−	−	−	⊥	±	++	++
niger, A, No. 1	++	++	++	−	−	±	++	++	++	++
niger, B, No. 1	++	++	++	−	−	±	+	++	++	++
carbonarius	++	++	++	−	−	±	++	++	++	++
awamori	o	o	o	o	o	o	o	o	o	o
cachuensis	++	++	++	−	−	⊥	++	++	++	++
sulverulentus	++	++	++	−	±	+	++	++	++	++
fumigatus, No. 1	++	++	++	−	⊥	±	++	++	++	++
oryzae	++	++	++	⊥	±	+	++	++	++	++
parasiticus	++	++	++	++	++	++	++	++	++	++
nidulans	++	++	++	⊥	⊥	+	++	++	++	++
versicolor	++	++	++	−	−	⊥	±	++	++	++
sydowii	++	++	++	−	−	⊥	±	++	++	++
ochraceus	++	++	++	−	−	⊥	±	++	++	++
Tamarii	++	++	++	±	±	++	++	++	++	++

Controls. *C.* 1. Complement + antigen + saline. *C.* 2. Complement + saline + immune serum. *C.* 3. Complement + antigen + normal serum.
− denotes complete fixation; ⊥ denotes good partial fixation; ± denotes partial fixation; ⊥+ denotes nearly complete haemolysis; ++ denotes complete haemolysis.

As shown by Table VIII the complement fixation took place most extensively when the anti-*Amstelodami* serum was tested with the homologous antigen. In testing with the other morphologically related antigens there was a certain degree of group reaction. In addition, some fixation was found in cross tests with any of the others except some particular species, viz. members of Group *D* and *A. Tamarii*. As is shown in Tables VIII, X, XI, XIII and XIV these species appear to be antigenically inert so far as complement fixation tests are concerned. Attention was then turned to the question whether these cross reactions were specific for the genus *Aspergillus*. Accordingly the antiserum was cross tested with *Penicillium glaucum* and *Gloeosporium fructigenum*.

Table IX. *Complement fixation of anti-*Amstelodami *serum with* Penicillium glaucum *and* Gloeosporium fructigenum.

Antigens	Controls			Serum dilution							
	C. 1	*C.* 2	*C.* 3	1:5	1:10	1:20	1:40	1:80	1:160	1:320	1:640
Aspergillus Amstelodami	++	++	++	−	−	−	−	−	−	−	⊥
Penicillium glaucum	++	++	++	++?	++	++	++	++	++	++	++
Gloeosporium fructigenum	++	++	++	+	++	++	++	++	++	++	++

See footnote to Table VIII.

From these results it is clear that *Aspergillus* serum gives little or no fixation of complement in the presence of *Penicillium* and *Gloeosporium*. With *Gloeosporium fructigenum* indeed some slight fixation was noted at the dilution of 1 : 5, while *Penicillium glaucum* could hardly fix the complement at the same dilution. This result is rather unexpected, because the *Penicillium* is more closely related to *Aspergillus* in morphological characteristics than is *Gloeosporium*. This will be further discussed later.

Table X. *Complement fixation with anti-*glaucus *serum.*

	Controls			Serum dilution						
Antigens	*C.* 1	*C.* 2	*C.* 3	1:5	1:10	1:20	1:40	1:80	1:160	1:320
glaucus, No. 1	++	++	++	±	±	+	+	++	++	++
glaucus, No. 2	++	++	++	±	±	+	+	++	++	++
Amstelodami	++	++	++	±	+	++	++	++	++	++
herbariorum	++	++	++	±	+	++	++	++	++	++
niger, A, No. 1	++	++	++	++	++	++	++	++	++	++
niger, B, No. 1	++	++	++	++	++	++	++	++	++	++
carbonarius	++	++	++	++	++	++	++	++	++	++
awamori	++	++	++	++	++	++	++	++	++	++
luchuensis	++	++	++	++	++	++	++	++	++	++
pulverulentus	++	++	++	++	++	++	++	++	++	++
fumigatus, No. 1	++	++	++	++	++	++	++	++	++	++
Oryzae	++	++	++	++	++	++	++	++	++	++
parasiticus	++	++	++	++	++	++	++	++	++	++
nidulans	++	++	++	++	++	++	++	++	++	++
versicolor	++	++	++	++	++	++	++	++	++	++
Sydowii	++	++	++	++	++	++	++	++	++	++
ochraceus	++	++	++	++	++	++	++	++	++	++
Tamarii	++	++	++	++	++	++	++	++	++	++

See footnote to Table VIII.

As already observed in the precipitation tests, the titre of the anti-*glaucus* serum was very low. Good partial fixation occurred only with the homologous antigens, and a slight group reaction at serum dilutions of 1 : 5 and 1 : 10.

The titre of this serum was very low, and therefore further inoculations of the same rabbit were made with increasing doses of the emulsified ground spores. The rabbit was bled on the ninth day after the fifteenth inoculation, and the complement fixation test was carried out with this new serum, but no marked difference was noticed.

In testing the anti-*niger*, A, No. 1 serum with some strains of *niger*, A and *niger*, B there was practically no differentiation between them. As already observed in the precipitation tests, these two types appeared to be identical in serological behaviour regardless of their biochemical differences. In connection with this experiment it is interesting to note that some of the antigens have shown serological reactions common to their own groups;

for instance, the Group *A* organisms show complete fixation at the serum dilution of 1 : 40, good partial fixation at 1 : 80 and complete haemolysis at 1 : 320, while the Group *C* fixed the complement at 1 : 80, and partial haemolysis at 1 : 320.

Table XI. *Complement fixation with anti-*niger, *A, No.* 1 *serum.*

	Controls			Serum dilution						
Antigens	*C.* 1	*C.* 2	*C.* 3	1 : 40	1 : 80	1 : 160	1 : 320	1 : 640	1 : 1280	1 : 2560
niger, A, No. 1	++	++	++	−	−	−	±	±	±	++
niger, A, No. 2	++	++	++	−	−	−	±	±	±	++
niger, A, No. 3	++	++	++	−	−	−	±	±	±	++
niger, B, No. 1	++	++	++	−	−	−	±	±	±	++
niger, B, No. 2	++	++	++	−	−	−	±	±	±	++
niger, B, No. 3	++	++	++	−	−	−	±	±	±	++
carbonarius	++	++	++	−	−	−	±	+	++	++
awamori	++	++	++	−	−	±	±	+	++	++
luchuensis	++	++	++	−	−	−	±	+	++	++
pulverulentus	++	++	++	−	−	−	±	+	++	++
Amstelodami	++	++	++	−	±	+	++	++	++	++
glaucus, No. 1	++	++	++	−	±	±	++	++	++	++
herbariorum	++	++	++	−	±	±	++	++	++	++
fumigatus, No. 1	++	++	++	−	−	±	±	+	++	++
fumigatus, No. 2	++	++	++	−	−	±	±	+	++	++
Oryzae	++	++	++	−	±	±	++	++	++	++
parasiticus	++	++	++	±	±	+	++	++	++	++
nidulans	++	++	++	−	−	±	+	++	++	++
versicolor	++	++	++	−	−	±	+	++	++	++
Sydowii	++	++	++	−	±	±	++	++	++	++
ochraceus	++	++	++	−	−	±	±	++	++	++
Tamarii	++	++	++	−	±	±	++	++	++	++

See footnote to Table VIII.

The next series of experiments were carried out to determine whether the reaction with anti-*niger*, A, No. 1 serum was absolutely specific for the genus *Aspergillus* (Table XII).

Table XII. *Complement fixation with anti-*niger, *A, No.* 1 *serum and* Penicillium glaucum *and* Gloeosporium fructigenum.

	Controls			Serum dilution					
Antigens	*C.* 1	*C.* 2	*C.* 3	1 : 20	1 : 40	1 : 80	1 : 160	1 : 320	1 : 640
niger, A, No. 1	++	++	++	−	−	−	−	±	±
Penicillium glaucum	++	++	++	±	+	+	++	++	++
Gloeosporium fructigenum	++	++	++	−	±	+	+	++	++

See footnote to Table VIII.

Table XII shows that, when anti-*niger*, A, No. 1 serum was tested with *Penicillium glaucum* and *Gloeosporium fructigenum* there was some fixation with both species. This result is rather curious, for it would be expected that the reaction would be more extensive with *Penicillium glaucum* than with the other,

if the serological affinities were correlated with the morphological characteristics. In this particular case, however, the result is quite contradictory. As already noted, a somewhat similar tendency was observed when anti-*Amstelodami* serum was cross-fixed with these species, but there the fixation was minimal (Table IX). It is concluded therefore that anti-*niger*, A, No. 1 serum contains, in addition to specific complement-fixing substances, several other such substances which are able to act on other fungi of different genera, though only in low dilutions.

Table XIII. *Complement fixation with anti-*niger, *B, No. 1 serum.*

	Controls			Serum dilution					
Antigens	*C.* 1	*C.* 2	*C.* 3	1:20	1:40	1:80	1:160	1:320	1:640
niger, B, No. 1	++	++	++	−	±	±	++	++	++
niger, B, No. 2	++	++	++	−	±	±	++	++	++
niger, B, No. 3	++	++	++	−	±	±	++	++	++
niger, A, No. 1	++	++	++	−	±	±	++	++	++
niger, A, No. 2	++	++	++	−	±	±	++	++	++
niger, A, No. 3	++	++	++	−	±	±	++	++	++
carbonarius	++	++	++	±	+	++	++	++	++
awamori	++	++	++	±	+	++	++	++	++
luchuensis	++	++	++	±	±	++	++	++	++
pulverulentus	++	++	++	±	++	++	++	++	++
Amstelodami	++	++	++	±	++	++	++	++	++
glaucus, No. 1	++	++	++	±	++	++	++	++	++
herbarium	++	++	++	±	++	++	++	++	++
fumigatus, No 1	++	++	++	+	++	++	++	++	++
Oryzae	++	++	++	+	++	++	++	++	++
parasiticus	++	++	++	+	++	++	++	++	++
nidulans	++	++	++	+	++	++	++	++	++
versicolor	++	++	++	+	++	++	++	++	++
Sydowii	++	++	++	+	++	++	++	++	++
ochraceus	++	++	++	±	±	++	++	++	++
Tamarii	++	++	++	+	++	++	++	++	++

See footnote to Table VIII.

As already observed in the precipitation tests the anti-*niger*, B, No. 1 serum proved to be very low in titre as compared with the anti-*niger*, A, No. 1 serum. Complete fixation was obtained only in the presence of the homologous strains.

Complement fixation with anti-*carbonarius* serum was best obtained in the presence of the homologous antigens. Fixation however was not confined to the group to which this fungus belongs. Practically the same amount of fixation occurred in all the remaining species with exception of Group *D*, viz. *A. Oryzae* and *A. parasiticus*. It is interesting to note that the members of this group are always antigenically inert so far as their use as antigen in the complement fixation test is concerned.

Table XIV. *Complement fixation with anti*-carbonarius *serum.*

Antigens	Controls			Serum dilution						
	C. 1	*C.* 2	*C.* 3	1:10	1:20	1:40	1:80	1:160	1:320	1:640
carbonarius	++	++	++	−	−	−	±	+	++	++
niger, A, No. 1	++	++	++	−	−	±	++	++	++	++
niger, B, No. 1	++	++	++	−	−	±	++	++	++	++
awamori	o	o	o	o	o	o	o	o	o	o
luchuensis	++	++	++	−	−	±	++	++	++	++
pulverulentus	++	++	++	−	±	++	++	++	++	++
Amstelodami	++	++	++	−	−	±	++	++	++	++
glaucus, No. 1	++	++	++	−	−	±	++	++	++	++
herbariorum	++	++	++	−	−	±	++	++	++	++
fumigatus, No. 1	++	++	++	−	−	±	++	++	++	++
Oryzae	++	++	++	+	++	++	++	++	++	++
parasiticus	++	++	++	++	++	++	++	++	++	++
nidulans	++	++	++	−	±	±	++	++	++	++
versicolor	++	++	++	−	−	±	++	++	++	++
Sydowii	++	++	++	−	±	±	++	++	++	++
ochraceus	++	++	++	±	±	++	++	++	++	++
Tamarii	o	o	o	o	o	o	o	o	o	o

See footnote to Table VIII.

Table XV. *Complement fixation of anti*-fumigatus, *No.* 1 *serum.*

Antigens	Controls			Serum dilution						
	C. 1	*C.* 2	*C.* 3	1:5	1:10	1:20	1:40	1:80	1:160	1:320
fumigatus, No. 1	++	++	++	−	−	±	±	++	++	++
fumigatus, No. 2	++	++	++	−	−	±	±	++	++	++
niger, A, No. 1	++	++	++	±	+	++	++	++	++	++
carbonarius	++	++	++	±	+	++	++	++	++	++
Amstelodami	++	++	++	±	+	++	++	++	++	++
glaucus, No. 1	++	++	++	±	+	++	++	++	++	++

See footnote to Table VIII.

As has been already mentioned, the rabbit inoculated with the spores of *A. fumigatus*, No. 1 died shortly after the eighth inoculation; therefore, no final tests could be made. A preliminary experiment showed, however, that complete fixation occurred only in the presence of the homologous antigen, or the strains of this species. In this respect the antiserum is highly specific.

Discussion.

A review of the results shows that agglutination tests are very unsatisfactory and unreliable as a means of differentiating these fungi. The principal cause of this unsuccessful result appears to be the difficulty of obtaining good spore emulsions. A large number of the spores in the normal sera settled within thirty to sixty minutes and formed a uniform layer on the bottom of the tubes in the same manner as in the immune sera. Some efforts were made to make good emulsions; for instance,

by thoroughly grinding the spores in order to get rid of the heavy spore walls, or by adding some glycerin to the spore suspensions, or mixing the spore suspensions with some bacterial emulsions. So far as the present experiments are concerned, however, no means appear to be successful. In tests with some antigens clumping of spores occurred in a noticeable degree, but owing to the low titre of the sera and the loose clumping of the spores no accurate reading of the agglutinating affinities could be made.

The precipitation tests with the filtrates are more satisfactory than the agglutination tests. The titre is certainly not so high as in ordinary pathogenic bacteria, and, moreover, the reaction is not highly specific. It is rather curious that there was no precipitation with any of the extracted spore materials. No interpretation of this negative result can be properly made at present, but it is suggested that there was probably very little antigenic substance in those spore extracts, since the materials used for the extraction were eight weeks' old spores grown on ordinary broth, consequently the larger amount of the reacting substances might be excreted from the organisms into the surrounding media.

There was no noteworthy difference in precipitation or in complement-fixing reaction between strains of *A. niger*, which, by their action on gelatin, could be differentiated into two types, viz. *liquefaciens* and *non-liquefaciens*, regardless of their morphological similarity. In this respect the serological behaviour of these fungi appears to be less specific than the biochemical character. The anti-*Amstelodami* serum appears to contain some complement-fixing substances which are able to act on any species of *Aspergillus* except some antigenically inert species, viz. *A. Tamarii* and the members of Group *D*. It is to be remembered, however, that in this particular serum there is little complement-fixing substance which reacts with other than *Aspergillus*, while the anti-*niger*, A, No. 1 serum contains, in addition to the specific complement-fixing substances, some other such substances which are able to act on species belonging to different genera, *e.g. Penicillium glaucum* and *Gloeosporium fructigenum*. So far as the anti-*Aspergilli* sera are concerned, the sera having a low titre appear to have a tendency to be more specific in precipitating and complement-fixing abilities than those having the higher titre. One plausible reason for this result may be, as suggested by Blakeslee (1915), that the last-named type of sera may have lost its specificity by receiving too many and too large immunising doses. In comparing anti-*niger*, B, No. 1 serum with anti-*niger*, A, No. 1 serum, it is noticed that the titre of the former is considerably lower than

that of the latter. This result may be due to the individuality of the rabbit inoculated.

Complement-fixation seems to be the most satisfactory method of differentiating these fungi, since the reactions are definitely observed in relatively high dilutions. However, the test cannot be utilised as a basis for the classification of *Aspergillus*, inasmuch as no apparent relation can be found in some particular instances between the complement-fixing reactions and the morphological characteristics.

Summary.

1. The purpose of the present investigation is to confirm to what extent the strains and the species of *Aspergillus* can be differentiated by serological methods. Immune sera were prepared from six different species, and each of these sera was tested with twenty-three species of *Aspergillus* and two species of other genera.

2. Agglutination tests were not successful, since no accurate reading of agglutinating affinities could be made.

3. Precipitation tests with filtrates proved more satisfactory than agglutination tests, but may have little application to the classification of *Aspergillus*.

4. Extracts of spores gave no precipitation with immune sera.

5. Complement-fixation tests proved the most promising of all, and may be utilised to identify or specify some particular *Aspergillus* to a certain extent, if the titre is taken into consideration. However, these tests cannot be adopted as a basis for the classification of *Aspergillus*.

6. The results of the precipitation tests agree with those of the complement-fixation tests in most important particulars.

7. Fixation of complement is accomplished more satisfactorily in a cold room than in an incubator, if the incubation period is extended overnight.

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SEEDS MIXTURES AND THE INCIDENCE OF FUNGAL DISEASE.

By E. Wyllie Fenton, M.A., B.Sc.

SEEDS Mixture is the name given to the mixture of grasses and clovers, and occasionally a few other plants, which the farmer sows in order to produce grassland. The grassland may be temporary or permanent, and the mixture differs according to which of these is desired. It is in the permanent type of grassland where any adverse condition is more evident, as it lasts over a long period, and also causes a greater financial loss.

The seeds used consist of varying proportions of several different species of grass seeds and two or three clovers. It may contain only a few species or several, in other words it may be a simple or a complex mixture (1). The important point is that from this mixture the farmer gets a herbage or an "artificial" association of plants, consisting of several grasses and probably at least two clovers (2). Some of the species are short lived and rapid growing, others longer lived and slower of growth. The ideal condition is where by maturing at different times they give a steady yield of green food throughout the greater part of the year (3).

During this time there is competition for space, light, moisture and food between plants of different habit of growth and different systems of rooting. Left entirely alone certain of the species would be crushed out by the others and disappear. It is obvious that the plants composing the mixture should agree and not compete too severely with each other; *i.e.* they should form a well-balanced mixture. The chief factor controlling this is the grazing of stock. Now it is the skill or otherwise of the

farmer in managing the grazing that makes or ruins a pasture (4). By skilful management and treatment the most desirable plants are encouraged and "the balance of power" maintained; in fact things may be much improved, and a poor pasture may thus become a good pasture. A well-balanced seeds mixture is however the foundation on which all rests.

Dealing with only one aspect of the inter-relationships of the components forming the pasture the case of grasses and clovers is most important. There is always keen competition between red clover and ryegrass. If one gains the advantage the other is almost suppressed or, at least, much reduced. Hence the proportion of each must be carefully balanced if both are desired, as they generally are, for the first year's cut of hay. There is another important point. Clovers have nodules on the roots in which are bacteria capable of fixing atmospheric nitrogen. Part of this is given to the soil with the decay of the nodules and the grasses benefit. After the early stages wild white clover occupies a considerable proportion of the pasture and continues to add nitrogen to the soil. A certain amount of material is added to the soil in the droppings of animals, but much depends on the age of the stock. Young stock retain from the vegetation lime, phosphates and nitrogen, older stock, except milch cows, do not retain much lime or phosphate (5, 6). Without going into further detail it is evident that nitrogen is one of the first things in which an unbalanced pasture tends to be deficient. The others with the addition of potassium will not be noticeable for some time, and the soil may have a sufficient supply of one or more of them. That is why in most pastures a good carpet of clover is so essential. It should also be remembered that White Dutch clover is short lived, not so resistant to disease and adds less nitrogen to the soil than wild white clover (7).

There is another important point regarding wild white clover. Its creeping stems which root at the nodes pass between the grasses and do not interfere with the normal habit of growth as the blades of the leaves come between the clover leaflets. Hence it is that the clover covers up and fills any bare spaces. This is most important when there is any likelihood of any dry spells producing a drought. Wild white clover covers the ground, shades it and therefore conserves the moisture. In any but a prolonged drought the plants growing with wild white clover are therefore able to obtain sufficient moisture, nitrogen and other foods. In the absence of wild white clover all except the deep-rooted plants are unable to obtain sufficient moisture or food. The deeper rooted plants can get some moisture but will be deficient in nitrogen and will find difficulty in obtaining sufficient lime, phosphate and potassium salts.

It is just under such conditions when the plants are not able to get sufficient nourishment, or are nourished on a badly balanced ration, that they are very subject to attacks by fungi, for like ill-nourished animals they are in a weakened condition and the power of resistance to disease is lowered. Of course an almost similar state of affairs may be induced by an excess of any of the food substances such as nitrogen. Many plants which are supplied with an excess amount of nitrogen and not sufficient other materials to balance the ration are frequently attacked by fungi. It may be mentioned incidentally that insect attacks are frequently primarily due to the same conditions.

To get a good example of the effect of a seeds mixture on the pasture, and the liability of one or more of the ingredients being attacked by fungi is not an easy matter. In the present case fortunately the whole history and treatment of the pasture is known.

In 1924 a field was divided into five plots of equal size, and each plot was sown down with a different seeds mixture. These plots have been regularly stocked, the stock carried by each being regulated by the amount of herbage given by the plots, so that every plot was worked under ordinary farm conditions. In addition a small portion of each plot was fenced off for hay so that a thorough comparison could be made.

The seeds mixtures used are given in Table I.

Table I. *Seeds mixtures sown.*

Plot	1 lbs.	2 lbs.	3 lbs.	4 lbs.	5 lbs.
Perennial ryegrass (Irish)	8	16	16	16	12
Italian ryegrass	8	—	—	—	4
Cocksfoot (New Zealand)	10	10	10	10	6
Timothy (Scotch)	4	4	4	—	—
Rough stalked meadow grass	—	—	—	—	1
Late flowering red clover (Suffolk)	4	4	4	—	—
English broad red clover	—	—	—	4	—
Trefoil	1	1	1	1	—
Wild white clover (Kent)	1	—	1	1	1
Dutch white clover	—	1	—	—	½
Cornish marl red clover	—	—	—	—	5
Total seeding per acre	36	36	36	36	29½

Late in the autumn of 1926 it was very noticeable that Plot 2 was very yellow, while every hay plot was of the same colour. This could be observed even from the top of neighbouring hills. This yellow colour was due to the presence of a rust (*Uromyces Dactylidis*) on Plot 2 and also on the hay plots of 1, 2, 3, 4 and 5. Owing to the severe drought the grass which was most evident was Cocksfoot; with the exception of No. 1, the proportion of

other grasses was very small. It was also noticed that the ryegrass in Plot 2 was slightly rusted (*Puccinia Lolii*), but that beyond occasional plants ryegrass was not affected in other plots.

If we consider the ground covered by each plant in June 1926 and late in October, we get the figures given in Table II.

Table II. *Area of ground covered.*

Plot	1	2	3	4	5
June:	%	%	%	%	%
Wild white clover	59	6	66	65	73
Ryegrass	28	22	21	22	17
Cocksfoot	8	44	5	9	6
Meadow grass	—	7	—	—	1
Timothy	5	7	1	1	—
Red clover	—	—	—	—	3
Bare	—	9	—	—	—
October:					
Wild white clover	32	—	3	8	12
Ryegrass	12	8	10	9	6
Cocksfoot	17	25	43	40	40
Meadow grass	—	9	—	6	—
Bare	36	58	38	37	34

It is evident that in Plot 2 the proportion of cocksfoot is high and wild white clover practically nil. In the other plots this is reversed. It will also be noticed that after the summer drought Plot 2 had far more space bare of vegetation than had the other plots.

The hay of all plots, by its tall growth, prevented the growth of any surface clover such as either wild white or Dutch white. Another point was that the red clover had died out the previous year, so that the hay consisted of grasses. The heat of the summer, after cutting for hay, scorched the soil between the growth of the grasses, so that all the hay plots suffered severely. Thus the sub-plots for hay suffered from both lack of nitrogen and lack of moisture.

Grazing, if properly managed, keeps the herbage short and gives wild white clover every chance to obtain light and keep level with other plants. Where this is not so the herbage becomes tall and coarse; clovers are crushed out and also the finer grasses, while weeds will probably appear. Continued neglect may lead to the formation of a mat of bent grass through which practically no other grass or clover can penetrate. The dead and dying vegetation accumulating on the surface of the soil makes it acid and ultimately almost approach a mild peat formation. In the present case the grazing was carefully watched and controlled, the number of stock (sheep and cattle) being varied

according to the capacity of the plot to supply herbage. So from the grazing point of view conditions were ideal.

It is obvious that in Plot 2 there were two factors responsible for the presence of rust: lack of sufficient nitrogen and lack of moisture. Exactly how much each factor contributed towards the disease it is impossible to estimate. It is very significant that exactly the same state of affairs was present in the hay sub-plots. I am indebted to my friend Mr A. Blenkinsop, for the soil nitrogen figures for the plots in Table III. It will be seen that in Plot 2 subsoil there is almost as much nitrogen as in Plot 4 and slightly more than in Plot 5. Plots 1 and 3 are higher. In the surface soil, however, it will be seen that Plot 2 is very much lower than all the others. As Plot 2 was the only plot without wild white clover, and the other ingredients differed very little in comparison, it is evident that the chief factor in the amount of surface nitrogen here is wild white clover. A glance at the surface of ground covered by wild white clover (as seen in Table II) in June and October, will show that the order is practically in complete agreement with the amount of nitrogen in the surface soil (as seen in Table III). At the present time (September, 1927) Plot 2 shows only slight traces of rust, but it is undoubtedly poorer than the other plots. The continuous rainfall of 1927 has kept the moisture factor out of the question. Still the disease is present and present only in Plot 2. The hay plots so far have not shown any trace of rust.

Another interesting feature of this rust attack in the autumn of 1926 was that it also occurred in several poultry runs. These runs were situated on part of an old but good pasture not very different in composition from that just considered. The grasses had been allowed to grow long and consequently wild white clover was not much in evidence. Cocksfoot formed the bulk of the grasses. Here the drought, although it must have had some effect, was not so severe, for the reason that the long vegetation was not cut and some clover was also present. Next, as the fowls had been running over the land for several years the droppings must have meant a heavy addition of nitrogen to the soil: much more in fact than would normally be the case. Here the presence of the rust is due to the excessive nitrogen manuring. The field generally had no rust on cocksfoot or on any other grasses. This presents the other side of the picture, where excess of nitrogen is the cause of the trouble (8). In 1927 there was no evidence of rust. The plentiful rainfall had doubtless enabled the grasses and clovers to obtain more lime, phosphate and potash, so as to "balance the ration."

There were some plants of cocksfoot rusted in Plot 2, but always in the open spaces where there was no wild white clover.

It was noticeable that where wild white clover had crept into the plot the cocksfoot plants were a deeper green and there was no trace of rust. Where dung had fallen in several plots it was noticeable that cocksfoot growing there was rusted. Here it was clearly due to excess of nitrogen, for the other plants quite near were free from rust. It is rather interesting that these two cases quoted for the autumn 1927 should verify so clearly the conditions of the autumn of 1926.

Table III. *The weight, in grammes, of nitrogen in* 100 *gm. of air-dried soil.*

	Nitrogen present	
Plots	Surface soil gm.	Subsoil gm.
1	0·370	0·269
2	0·347	0·248
3	0·360	0·266
4	0·365	0·251
5	0·395	0·246

Conclusion.

No. 2 is the only plot which suffered. In areas where dry spells are a danger wild white clover is invaluable both for nitrogen supply and conservation of moisture. In pasture plants a pathological state generally originates with unfavourable physiological conditions. Such conditions usually can be avoided by the use of a well-balanced seeds mixture suitable to the soil and general conditions of farming practice.

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NOTE ON RHIZOCTONIA CROCORUM (PERS.) DC.

By W. M. Ware, M.Sc.

As has been recorded (1), *Rhizoctonia violacea* (recte *R. Crocorum*), the cause of violet felt rot of various crops, amongst others sugar beet, mangolds, lucerne, potatoes and carrots, was found in November, 1922, attacking red clover. The fungus had not previously been reported on red clover in this country.

At the beginning of April, 1923, *Helicobasidium purpureum* (Tul.) Pat. was found on the same red clover crop as that on which the *Rhizoctonia* had first been seen—an observation which was then important in view of the possibility that *Helicobasidium* might prove to be the perfect spore-bearing stage of the sterile fungus *Rhizoctonia Crocorum* (2, 3).

It was intended that the field in which the violet felt rot occurred should not again come under red clover until after a period of eight years, in order to avoid loss by clover stem-rot (*Sclerotinia Trifoliorum*). In the fourth year, a mixture of white clover (*Trifolium repens*) and trefoil (*Medicago lupulina*) was sown. The field had been examined each year after 1922 but not at regular intervals. On March 23rd, 1927, patches of the ley, each about one yard in diameter, were found to be affected in a similar manner to that described for red clover in 1922 (1). Examination showed that trefoil plants were attacked and were often loose on the surface of the ground, their main roots having rotted away. Numerous plants with the "corps miliaires" of the fungus were found. In addition, felted mycelium of *Rhizoctonia* covered many of the more prostrate stems and in association with this, *Helicobasidium purpureum* here and there occurred on stems and stipules. White clover was not found attacked.

The system of cropping on the field mentioned had been as follows: 1923, Red Clover, sown April, 1922; 1924, Winter Oats, sown October, 1923; 1925, Mangolds and Swedes, sown May, 1925; 1926, Barley, sown April, 1926; 1927, White Clover and Trefoil, sown April, 1926.

The present case is of special interest because in one and the same field, *Rhizoctonia* occurring on *Trifolium pratense* and later on *Medicago lupulina* (both presumably first records for this country) has on both occasions been followed in the spring by *Helicobasidium purpureum*. This record of the association of *Helicobasidium* with *Rhizoctonia Crocorum* on trefoil is supplementary to those on other hosts mentioned by W. Buddin and E. M. Wakefield (3). The apparent persistence of the disease

provides some circumstantial evidence against the view that the genera *Trifolium* and *Medicago* are attacked by biologic forms of the fungus.

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FIELD NOTES ON AN ATTACK BY RHIZOCTONIA CROCORUM ON SITKA SPRUCE (PICEA SITCHENSIS).

By H. Watson, Beaufort Forest School.

On visiting a forest nursery at Beauly, Inverness-shire, at the end of April, 1928, I was struck by the number of dead patches in two areas of Sitka Spruce (*Picea sitchensis*). Although, after two trying winters, there had been many deaths of this species in forest nurseries, the "yellowing" of the plants on the circumference of these patches indicated that some trouble additional to frost damage was present.

Examination of specimens showed the "collar" to be surrounded by a violet coloured, velvet-like fructification* which frequently encircled some of the small lower branches, and also spread over the surrounding soil. The roots showed definite signs of rot, and, on slipping them between the fingers, the cortex came away leaving the brown stained wood. Strands of mycelium could be detached easily from the roots, and, under a hand lens, showed a pronounced purple-brown colour, while studded over the bark of the roots could also be seen small black dots—the "infection cushions" typical of *Rhizoctonia Crocorum*.

The Sitka Spruce had been "lined out" as two year old seedlings in the spring of 1926 at two inches apart with ten inches between the lines, so that, at the time of the visit, they were 2 × 2 plants, *i.e.* two year seedlings lined out for two years. Many of the plants grew nine inches in height during the 1927 season, and were quite normal in size for the district, being sixteen to twenty-four inches high.

The land grew a crop of potatoes in 1922 immediately before being taken into the nursery, and has had no manure, or green cropping, since that time. Scots Pine was lined out in 1923 and again in 1924, followed by European Larch in 1925 and the

* See note immediately following by W. Buddin and E. M. Wakefield.

Sitka Spruce in 1926. The field lies just below the 100 ft. contour, and is an acid sandy loam with a northerly aspect, but well sheltered from all directions. The most prevalent weeds are sheep's sorrel (*Rumex Acetosella*) and white clover (*Trifolium repens*), which is exceptional in such abundance in nursery lines. The clover was a healthy green and showed no traces of root attack, but a good deal of the sorrel was dying and the roots showed numerous "infection cushions." The two infected areas in this nursery were 630 sq. yds. and 264 sq. yds. in extent respectively. In the first area there were six points of infection, each averaging 10 sq. ft., and thirty small points of a few plants each. In the second area one-fifth of the plants were dead. In another small nursery five hundred yards distant only one plant showed the violet coloured fructification.

The following details from the meteorological records at the Forest School in the vicinity of the Nursery may be of interest. During the first year after transplanting of the Sitka Spruce frost was registered on 134 days, while during their second year (1927–28) there was frost on 119 days. Temperatures as low as 14° and 16° F. were recorded on four days during the first winter, and there were minima of 18° F. on April 29th, 24° F. on May 11th and 27° F. on June 15th, 1927. The frost on May 11th left all the Forest School Nursery brown; the majority of the Sitka Spruce shed their needles, and it was late in the season before the new shoots clothed the plants. In December, 1927, occurred the most severe frosts on record. The temperature fell to zero on December 29th, and on five other days in the month the minimum was from 6° to 8° F., with 14 to 22 degrees of frost on four further days. The rainfall was 31·8 inches in 1926–27, and 48·5 inches in 1927–28.

If frost damage is one of the necessary predisposing factors for an attack of the disease on Spruce, it is unlikely that it will ever be a factor which is absent. Even in average seasons traces of frost damage are always found with this species, and, during the seedling stage, protective covering in winter is essential. Care should be taken to avoid the use of seed from the more southerly parts of its habitat.

The ability of the fungus to utilise weeds as a host-plant makes it very difficult to eradicate from nurseries, as the burning of the Sitka Spruce, and even the resting of the ground with a green crop, would have little effect in checking the fungus. Since Sitka Spruce is our most hopeful exotic, and the cost of rearing is very heavy, the outbreak of the disease on this species is economically serious.

FURTHER NOTES ON THE CONNECTION BETWEEN RHIZOCTONIA CROCORUM AND HELICOBASIDIUM PURPUREUM.

By W. Buddin and E. M. Wakefield.

Since the publication of the paper by the authors (1) on this subject some further confirmatory observations have been made which it seems advisable to place on record.

Early in April, 1927, Mr W. M. Ware reported the occurrence of *Helicobasidium purpureum* in association with violet root rot of black medick (*Medicago lupulina*). This was in the same field at Wye, Kent, as that which had shown, in 1923 in the previous rotation, the red clover disease recorded in our paper. Mr Ware's note (2) gives details of his field observations. From material kindly supplied by him, pure cultures were obtained as before from (*a*) "corps miliaires," or infection cushions, of *Rhizoctonia Crocorum* on the roots, and (*b*) spores of the *Helicobasidium*. In general behaviour, *e.g.* slowness of growth, particularly from spores; difficulty of isolation from single spores; variability in appearance from time to time, and abundant production of conidia in recently isolated "spore cultures," these isolations agreed with those previously obtained from other hosts.

During the summer of 1927 inoculations, though not on so large a scale as previously, were carried out with these cultures on mixed Leguminosae and carrots sown in sterilised soil. The isolations from the "corps miliaires" gave rise to a certain number of infections. In three pots of carrots, inoculated at the time of sowing (May 28th) and examined towards the end of September, roughly fifty per cent. of the roots in each pot showed infection cushions. With mixed clovers sown in May, but not inoculated until July 4th, and examined at the end of September, the number of successful infections was very much less. A second pot examined later (November 26th) gave better results, showing eight infected plants out of thirty. Probably the vigour of the mycelium used for inoculation, and the stage of development of the roots, as well as the temperature and the period of time elapsing before examination, are all factors influencing the success of the inoculation experiments. Cultures derived from spores of the *Helicobasidium* unfortunately gave rise to no infections.

At the same time inoculations were carried out with other strains of *Rhizoctonia*. It is possibly partly owing to the length of time *in vitro* from the original isolations, but it is to be noted that no infection has yet been obtained with the strain of

R. Crocorum isolated by Wollenweber from *Beta vulgaris*, received through the Centraal-bureau voor Schimmelculture, Baarn, nor has a strain of *R. Crocorum* isolated from cotton, in Trinidad, by Professor H. R. Briton-Jones, given positive inoculation results. However, this cotton strain is of especial interest in connection with this work. On receipt of the original tube from Trinidad by the Imperial Bureau of Mycology, sub-cultures were made by Mr Ashby to autoclaved corn meal in Erlenmeyer flasks. After some weeks one of these sub-cultures produced pustules of *Tuberculina*-like conidia, resembling exactly those already described by us (*loc. cit.*) as occurring in most "spore cultures," and in the isolations from "corps miliaires" from mangold and from nettle.

The later results thus support the position taken up in the previous paper, namely that strains of *Rhizoctonia* from different host-plants vary considerably in virulence, and that the difficulty in obtaining positive inoculation results from spore-isolations may be due partly to the existence of weakly parasitic strains. Little is known with precision concerning the conditions favouring attack by *R. Crocorum*. Under the conditions of our experiments the leguminous plants have been always sufficiently vigorous to develop abundant adventitious roots, and no yellowing of the tops of affected clover plants has been noted. It is possible that the comparatively vigorous condition of the host-plants explains in part the regrettably small proportion of positive inoculation results with weakly parasitic strains obtained from spores. It is further to be noted that strains of *Rhizoctonia* which produce conidia appear to be less strongly parasitic than those which do not, and that successful infections with spore-isolations have been obtained only from non-conidia-producing cultures.

Recently (May, 1928), confirmatory evidence of the connection between *Helicobasidium purpureum* and *Rhizoctonia Crocorum* has been obtained from a new source and on an entirely different host. Through the courtesy of Mr J. S. L. Waldie of the Agricultural Botany Department, Reading University, who kindly handed over the specimens, we obtained material of young Sitka Spruce which had been sent in by Mr H. Watson of the Beaufort Forest School, Kiltarlity, Beauly. Ten plants were received and in each the roots showed typical symptoms of violet root rot (3). Many of the badly rotted roots had lost their cortex, and others showed plainly the mycelium and "corps miliaires" of *Rhizoctonia Crocorum*. With nine of the ten plants the collar was encircled by the violet fructification of *Helicobasidium purpureum*, and the connection of this with the mycelium on the roots below was unmistakable.

The evidence recorded here supplements the previous field, cultural and inoculation work. We consider that any present inconsistencies will be explained with better understanding of the various strains, and of the conditions favouring vigorous infection with this fungus, and that there is no doubt that *Helicobasidium purpureum* is the perfect stage of *Rhizoctonia Crocorum*.

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RHIZOCTONIA BATATICOLA AND TEA ROOT DISEASES.

By C. H. Gadd, D.Sc.
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The discovery of *Rhizoctonia bataticola** on the roots of a large number of woody plants in Ceylon and Uganda has led Small (9) "to more or less unorthodox ideas on the causation of root disease in Ceylon." His views are briefly summarised in the following sentences. "There are legitimate grounds for a reconsideration of previous ideas of the causation of root disease in Ceylon, and in that reconsideration the part played by *R. bataticola* must be recognised" (9). "*Rhizoctonia bataticola* must be regarded as a destructive parasite of woody plants and trees, in fact, as the only parasite of present importance in the causation of root disease and its secondary results" (7). Such fungi as *Ustulina zonata*, *Fomes lignosus*, etc., which have been regarded as root parasites of primary importance, not only in Ceylon but elsewhere, are thus relegated to a secondary position; their "supposed parasitic status" is doubted (9). *Rhizoctonia* "is the primary parasite without the work of which the secondary fungi would be unable to attack" (8).

The idea of successional disease is neither new nor unorthodox. The unorthodoxy of Small's views is to be found in the attribution of greatest importance to the fungus with the least evidence of parasitism, and in the proofs he offers of the parasitism of this fungus. It is also somewhat unusual, especially after but a few months' acquaintance of the conditions and

* The name *Rhizoctonia bataticola* (Taub.) Butler is used throughout this paper in preference to the probably more correct one, *Macrophomina Phaseoli* (Maubl.) Ashby, as the vegetative state only of the fungus is under consideration.

fungi of a country, to doubt the parasitic status of a large number of root fungi, in fact practically every fungus which has been stated to be parasitic on roots in Ceylon, in order to advance the claims of another.

R. bataticola has long been known to be associated with certain diseases of herbaceous plants such as jute, cotton seedlings, ground-nut, etc. Small accepts its parasitism on herbaceous hosts as proved, but Briton Jones (1) maintains that "there has been considerable evidence put forward by different mycologists that the fungus *Macrophomina Phaseoli* becomes parasitic on adult plants only under special conditions. The conditions are such that they in themselves thoroughly upset the metabolism of the plant before it is attacked by the fungus."

In this paper we are concerned only with the parasitism of *R. bataticola* to woody hosts, of which there is already an extensive list. The writer proposes to confine his observations entirely to one host plant, viz. Tea, with which he is intimately acquainted, and which is one of the most important listed by Small whose statement concerning the root diseases of this plant is very definite: "*R. bataticola* may thus be regarded as the primary agent which prepares the way for other fungi and it follows that *Ustulina* and the other fungi on tea...are secondary" (9).

This statement is unsupported by any experimental evidence, and field observations do not justify the conclusion. Petch (5) has briefly reviewed the experimental evidence of the parasitism of the tea root disease fungi, thus arbitrarily relegated to a secondary position, from which it appears that there is far more evidence than Small admits. Attention will, therefore, be confined mainly to the field evidence.

Small records that of two hundred and sixty-three cases of tea root disease, examined between the beginning of May and the end of September, 1926, one hundred and forty-six were clear cases of attack by *R. bataticola* alone. He has omitted to state what symptoms accompanied the disease in the field. It is within the writer's knowledge, as he saw a large number of these specimens, that the majority of, if not all, these cases would have been diagnosed previously as "*Diplodia*" root disease.

The peculiarity of the so-called *Diplodia* root disease of tea in Ceylon is that it almost invariably occurs after pruning. The diseased bushes are scattered haphazard through the fields and are not restricted to particular areas. Field diagnosis is usually based on the facts that the diseased bush makes little or no recovery after pruning, although it appeared perfectly healthy before, and that other known root disease fungi, such as *Poria*

hypolateritia, Rosellinia arcuata, etc., are absent from the roots. The affected bushes sometimes put out new shoots which may grow to a length of about six inches, when the leaves turn yellow, the shoots die back to the base, and the bush dies. Bushes which survive this critical stage, although slow in producing new shoots, make good growth later and there is no further recurrence of the disease till next pruning time. Bushes in full leaf are never affected by this form of *Diplodia* disease.

The name "*Diplodia* disease" is an abbreviation of *Botryodiplodia Theobromae,* a fungus which is usually to be found on the roots of affected bushes. The disease is known in India and Java, where it is also ascribed to the fungus *Botryodiplodia Theobromae.*

The fact that deaths occur only after pruning suggests the possibility of the disease being caused by physiological factors associated with pruning. There is evidence to support this view. In tea cultivation, the young leaves are plucked from the bush at intervals of ten days or less, and the bush is pruned back at intervals of three years or less. At low elevations, where this disease is most prevalent, the plucking rounds occur as a rule at intervals of about seven days, and the pruning cycle never exceeds two years. At higher elevations, where climatic conditions do not induce such rapid growth, plucking and pruning occur at longer intervals. In these districts the disease is very rare, though both *Rhizoctonia* and *Botryodiplodia* are by no means uncommon fungi. When pruned, the bushes as a rule are entirely denuded of leaves. Consequently, the bush is dependent upon stored food reserves for all new growth.

During the course of my investigations, I have found that the roots of bushes affected by the so-called *Diplodia* disease contain little or no starch, whereas normally healthy bushes contain ample starch reserves in their roots. Roots form the main storage regions for reserve foods of the tea plant. It would appear, without dogmatising on the subject, that a deficiency of reserve food will account satisfactorily for the death of certain bushes after pruning, without invoking the aid of any fungus parasite. When dead or moribund it is reasonable to suppose that the roots of such bushes become invaded by soil saprophytes, amongst which *Rhizoctonia* and *Botryodiplodia* for the time being may be included.

Small's claim that the one hundred and forty-six cases referred to were attacked by *Rhizoctonia* alone is somewhat incomprehensible, not because of the above suggested physiological explanation of their deaths, but because of the absence of *Botryodiplodia,* which, owing to its constant association with this disease, has elsewhere been considered to be the cause of it.

There can be no mistake that what I have here called "*Diplodia*" disease is also the pathological condition Small refers to, for he writes: "Sudden deaths of tea bushes after pruning have been shown to be due to *Rhizoctonia* root disease, the presence of which was not suspected until the plants died apparently as the result of pruning" (9). In addition to the one hundred and forty-six cases of *Rhizoctonia* alone, he mentions forty-six in which *Botryodiplodia* was associated with *Rhizoctonia* and twenty-six in which *Botryodiplodia* occurred without it. As *Botryodiplodia* would be recorded only when its fructifications were found, whereas *Rhizoctonia* is identified by its sclerotia and mycelium, the evidence in favour of *Rhizoctonia* being the primary cause of this disease is, thus, very little stronger than that in favour of *Botryodiplodia*. It is unnecessary, however, to enter into a discussion of the relative merits of these two fungi in the causation of this disease, particularly as there is good reason to believe that the disease is due to physiological causes.

It is, however, evident on Small's own showing that *R. bataticola* is not "constantly and abundantly associated with the disease or pathological state" said to be due to this fungus. This is the first requirement of the rules of proof formulated by Koch as quoted by Duggar (2). Small has nowhere attempted to show that *R. bataticola* is constantly and abundantly associated with any particular disease; instead, he has shown that it is associated at times with all root diseases and many stem diseases, and has based his claims for its parasitism on this. Consequently, he claims that *Rhizoctonia* is the primary cause of all root diseases, and not merely the cause of a particular one.

Small has substituted new so-called proofs for the generally accepted ones. The chief of these is, "When only one fungus is concerned in a root disease, the responsibility for the disease ought to be placed upon that fungus" (9). Stated thus, everything depends upon what is meant by the term "concerned in a root disease." Referring to root diseases in Ceylon, he has stated that they may be divided into two classes. "The first of the classes is those cases in which one fungus only is concerned, and the second those in which more than one fungus is present" (7). "One fungus only is concerned" obviously means that one fungus only is present. This interpretation is confirmed by his frequent use of the term "sole association." Sole association is regarded by him as a primary proof of the parasitism of *R. bataticola*.

He also appears to consider that the proof of parasitism of other root fungi has also been based on a claim of "sole association." In a reference to *Poria*, *Rosellinia* and other root

fungi the following statement occurs: "The parasitism of the fungi has been assumed on the ground that each is in constant sole association with a certain diseased condition" (9). The assumption is exclusively Small's. If constant sole association were necessary as an essential proof of parasitism of root fungi, the list of known parasites would be reduced considerably; in fact it is unlikely that any name would be left on the list. In my experience, no single fungus is ever found in constant sole association with a tea root disease.

Small has attempted to explain this by stating that "the words 'sole association' are not used in an absolute sense" (8). The relative meaning of this term is explained in the following sentences. "The fungi associated with a case of root disease, particularly of a woody plant, can be divided into two groups, major and minor. An experienced mycologist will have little difficulty in deciding...which fungi shall be placed in one group and which in the other" (8). An arbitrary classification of this nature no doubt has its uses. To describe a fungus which is placed alone in the major group as being in "sole association" with a disease and to refer to the disease as a "simple one fungus example" is certainly misleading. It would appear doubtful that any reader has interpreted the terms "sole association," "occurs alone," "simple one fungus examples of root disease," etc., in the so-called "relative sense" that Small has stated was intended.

Reference has already been made to Small's division of root diseases into two classes. Concerning the first of these classes, in which one fungus only is concerned, he states: "The single one fungus examples of root diseases are not cases of *Fomes* or *Ustulina* or *Diplodia* or *Poria* or *Rosellinia*; they are cases in which *Rhizoctonia bataticola* is present and they are simple in the sense that the *Rhizoctonia* alone is to be blamed for the loss of the diseased tree or bush" (7). Of the second class he says: "In the case of the second class, that in which more than one fungus is present, it is to be noted particularly that *Rhizoctonia bataticola* has been found to be present in every case" (7). There would thus appear to be no root disease in Ceylon with which *R. bataticola* is not associated, either alone or in association with other fungi.

In this connection, an examination of the statistics of tea root diseases given by Small is of interest. He mentions one hundred and forty-six specimens of clear cases of *R. bataticola* alone, sixty-six in which *Rhizoctonia* was accompanied by other fungi, and fifty-one with which *Rhizoctonia* did not occur. The fifty-one specimens consisted of fifteen of *Poria*, one of *Fomes lamaoensis*, eight of *Ustulina*, one of *Rosellinia*, and twenty-six

of *Diplodia*. These cases are excluded by name from the first of Small's classes, and they cannot belong to class two, unless he is in error when he particularly states that *R. bataticola* has been found to be present *in every case* in this class. There is thus a third class of root diseases which comprises those cases with which *R. bataticola* is not constantly associated, and concerning which no mention has been made. In this class are to be found cases of *Poria, Fomes lamaoensis, Ustulina, Rosellinia* and *Diplodia*, in fact all the major root diseases of tea. If then, the existence of this class is admitted, as undoubtedly it must be, even on Small's own showing, the claim that *R. bataticola* is the primary parasite without the work of which *Poria hypolateritia*, etc., are unable to attack is unfounded, and any hypothesis built upon this assumption must fall.

Small's figures showing that "over fifty per cent. (of the tea root diseases examined during a certain period) were clear cases of attack by *R. bataticola* alone" (9) do not give a true representation of the incidence of tea root diseases in Ceylon. The majority of these cases were sent in for examination, by the cart load, from a small area of tea on the Peradeniya Experiment Station. These bushes had died after pruning. The heavy consignments of this one disease from one place undoubtedly loaded the percentage figures. Usually an estate sends one or two bushes only, representative of the diseased area; consequently, one specimen sent from an estate other than the Peradeniya Experiment Station may be representative of a large number of bushes similarly attacked; and, if all the specimens were received from the Experiment Station, which is very doubtful, his records refer to that estate only. In any case, his figures certainly give a very wrong impression of the incidence of the various diseases in Ceylon generally.

Turning now to the statements concerning other root diseases of adult tea, reference need be made only to four of the commonest, viz. those caused by *Poria hypolateritia, Rosellinia arcuata, Ustulina zonata* and *Fomes lamaoensis*. Concerning these he states: "I have found them only on the plants which have been affected directly or indirectly by the *Rhizoctonia*" (9). This statement is not borne out by his own figures, as he mentions only two cases of *Poria* accompanied by *Rhizoctonia* and fifteen of *Poria* alone. The corresponding figures for *Rosellinia, Ustulina* and *Fomes lamaoensis* are five and one, seven and eight, and three and one respectively.

The *Poria* and *Rosellinia* diseases in tea usually occur in patches. The diseases spread outwards from a centre, and large bare areas are left when the dead bushes have been removed. Each year, the affected areas become larger unless the progress

of the disease is checked and dead and dying bushes are to be found on their perimeters. Vigorous bushes are attacked at any stage in the pruning cycle; the diseases are not confined to pruned bushes. The spread of these fungi is so characteristic that it is often possible to state with certainty that one of them is concerned before a bush is uprooted for examination. *Rhizoctonia*, on the other hand, "has not produced any evidence of its spread by contact" (6). How, then, can the spread of a fungus like *Poria* be accounted for on Small's hypothesis? This point has not been considered, but some explanation appears necessary before *Poria* is relegated to a secondary position, in favour of the non-spreading *Rhizoctonia*. *Poria hypolateritia* is the commonest root fungus on tea in the Ceylon up-country districts, and the evidence of its spread by contact is indubitable.

When a tea bush, affected by the *Poria* or *Rosellinia* disease, is lifted from the soil, it is usual to find several of its main lateral roots badly rotted. Frequently, the bush is not killed until the collar region is affected. The tea bush is difficult to kill, and very few trees or shrubs could withstand the treatment meted out to it in cultivation. Yet we are given to understand that the presence of *R. bataticola* on a few rootlets is of far greater importance, pathologically, than the rotting of the laterals and tap root by fungi like *Poria* and *Rosellinia*. The absence of some of the smaller roots of specimens has been one of the difficulties in establishing the invariable presence of *Rhizoctonia*. "The common lack of small roots is of greater consequence than the cloaking action of the other fungi, especially since it often happens that only a small proportion of the roots of a plant is attacked" (9). If the destruction of a small proportion of the roots of a tea plant is of such vital importance, the wonder is that the bushes of a tea field ever survive the cultivation of the soil by forking.

Small stresses the fact that *Rhizoctonia bataticola* attacks *via* the fine rootlets, and deduces therefrom "that the probability of its priority of attack is greater than that of other fungi" (9). Few mycologists will agree that an invasion of the finer rootlets is the "more natural mode of attack," or that fungi cannot penetrate the larger woody roots until the finer rootlets have been invaded. These assumptions loom largely in the arguments put forward for a reconsideration of the status of *Poria*, *Rosellinia*, etc., as parasites, but obviously they prove nothing.

The root diseases caused by *Ustulina zonata* and *Fomes lamaoensis* do not affect large patches of tea. Almost invariably, they are associated with stumps. Small says: "I have not found the stumps and other sources or jumping off places of fungi like *Fomes lignosus* and *Poria* which are indicated in the literature,

nor the contact said to be necessary for the spread of *Fomes lamaoensis* to living roots" (9). He has, however, omitted to state that for the last quarter of a century, the digging out of jungle stumps has been a routine practice on many estates in Ceylon. During the experience which I have had of tea in Ceylon there has been a marked diminution of the incidence of *Ustulina* and *Fomes lamaoensis*, which, in my opinion, can only be ascribed to the removal of stumps. Both diseases are rarely found nowadays in old tea, except after shade trees have been cut out and the stumps left in. The diseases, however, are not uncommon in new clearings. I have yet to find a specimen of *Fomes lamaoensis* in the field which cannot be traced directly to an old stump. Small's experience of this disease in Ceylon is peculiar, if he has not found "in the course of many excavations" the contact between living roots and infected stumps necessary for the spread of this disease. *Poria* patches are usually quite bare, and it is impossible at this late date to say where the disease originated. If the disease originated at a stump the stump was probably dug out when the first dead tea bush was removed. Though frequent references to stumps may be found in the literature of Ceylon root diseases, the possibility of infection by wind-borne spores has by no means been neglected.

Old stumps can be found abundantly in any jungle clearing of young tea. An investigation of the root diseases of such clearings provides abundant evidence of the importance of such stumps in the causation of disease. The evidence of spread by contact even from jungle stumps is against Small's hypothesis of the causation of these diseases, but the denial of the existence of the stumps does not improve the case.

Small also claims that "*R. bataticola* has been found to kill tea seedlings in nurseries and young plants in new clearings" (9). He has recorded the presence of *Rhizoctonia* on the dead roots of seedling plants, but he has produced no evidence that this fungus killed them. It should be noted that, throughout his writings, the presence of *Rhizoctonia* on dead roots is considered to be synonymous with proof of parasitism.

No mention is made of the general symptoms exhibited by the young plants claimed to have been killed by *Rhizoctonia*, and therefore it is impossible to recognise which seedling disease is referred to. The commonest diseases of tea seedlings are those known as "Bitten off" and "Collar rot." In the former, the roots rot, and when pulled from the soil they have the appearance of having been bitten off. Collar rot is characterised by a destruction of the external tissues of the stem at ground level. Neither of these conditions has been caused experimen-

tally by inoculation with *Rhizoctonia* or any other fungus isolated from diseased roots. These diseases are probably the result of physiological causes. Bitten off can be induced by unsuitable water relations. Seedlings affected by Collar rot frequently recover, new stems being produced from below the rotted area, particularly if the plants are transplanted to more favourable situations. This disease, therefore, is unlikely to be caused by fungi within the root system.

Because *Rhizoctonia* is not always to be found on plants affected by Collar rot we are told that there is more than one cause of the disease, and that "the collar rot is entirely a secondary phenomenon" (9). Collar rot is not unknown as a pathological condition of seedlings other than tea. The literature on these diseases gives no indication that collar rot is a secondary symptom, or that it is the result of fungus attacks on the root system.

Ustulina, Poria and other fungi, except *Rosellinia arcuata*, commonly associated with root disease in old tea, are unknown on seedlings. The last-named fungus has been found in very few cases and those occurred recently. Inoculation experiments* on tea seedlings proved conclusively that *Rosellinia arcuata* is a virulent parasite and will kill seedlings without the aid of *Rhizoctonia* or other fungus. These experiments also demonstrated that this fungus will not attack the fine roots; its attention is confined solely to woody parts. Since it has been shown that a preliminary attack on the finer roots is unnecessary before *Rosellinia* can attack the tap root or collar of a tea plant, there appears to be no *prima facie* reason why an invasion by *Rhizoctonia* should be necessary before certain other fungi can attack also.

There appear to be no macroscopic characters by which the *Rhizoctonia* disease, if such occurs, can be recognised. Small says: "Small roots which are dead and hard and firm and which show transverse cracks in the bark should be suspected of *Rhizoctonia* attack" (7). The wood of tea roots is normally very hard, and when healthy tea roots are allowed to dry, the cortex cracks transversely. Transverse cracks in dead tea roots and stems are very common, but I have not found *Rhizoctonia* to be always associated with the symptoms. The presence of black lines in diseased tea wood, as Small admits, does not signify the presence of *Rhizoctonia*. There is thus no means of identifying the so-called *Rhizoctonia* disease in tea, other than by careful microscopic examination of all the fine rootlets. The omission of a description of the symptoms exhibited by tea plants killed by this fungus alone and unassisted by

* See *The Tea Quarterly*, vol. 1, Part 3 (in the Press).

any other fungus or adverse environmental condition, is to be regretted.

In view of the observations of Tunstall (10) and Park (4), the presence of *Rhizoctonia bataticola* on dead tea roots is no indication whatever that this fungus contributed in any way towards causing the death of the plant. Tunstall recorded the presence of a mycorrhizal fungus within tea roots in India, and Park has confirmed this observation in Ceylon. Park has further identified the mycorrhizal fungus as *R. bataticola*. The identification has been made in the laboratory of which Small is in charge, so it is to be assumed that he concurs. As *R. bataticola* is present within normally healthy tea roots it is likely to be found within dead tea roots also, no matter what may be the direct cause of their death. When the roots die, the fungus becomes saprophytic, forms sclerotia, becomes more abundant and is more easily identified. These observations offer a simple explanation of the presence of *Rhizoctonia* in the fine rootlets of dead tea bushes and seedlings, but they do not support the claim that the *Rhizoctonia* killed the plants. In fact, the whole of Small's arguments fall to pieces.

Although the mycorrhizal theory explains Small's observations regarding the presence of *R. bataticola* on dead tea roots, and possibly those of coconut and *Hevea*, it does not, as yet, account for its presence on the roots of numerous other plants. The suggestion that the observed facts may be accounted for on the basis of saprophytism (3) has been somewhat summarily dismissed by Small, because "the fact that it (*R. bataticola*) is often the sole cause of root disease and subsequent death is against the theory of its saprophytism" (9). An assumption of parasitism, however, cannot be held to disprove saprophytism. That *Rhizoctonia* is often the sole cause of root disease in tea cannot be maintained, even on the facts adduced by Small. When the results of the inoculation experiments are produced, it is hoped that the existence of the mycorrhizal fungus will not be overlooked. If the parasitic theory of mycorrhiza be accepted, some account of the causes which upset the equilibrium and turn the symbiont into a true parasite will be required.

As the evidence stands at present, I see no reason for supposing that *R. bataticola* ever causes a pathological condition of tea. Small has admitted that he is "tempted perhaps to make for *Rhizoctonia* larger claims than are justified in the meantime," but he does not appear to be aware of the extent to which he has misrepresented facts to advance those claims. For this reason it appears necessary to point out that the statements regarding the causes and incidence of diseases in Ceylon made

by him do not represent the opinions or experience of other mycologists in Ceylon, in particular those of the Tea Research Institute.

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OBSERVATIONS ON THE SPREAD OF THE APPLE MILDEW FUNGUS, PODOSPHAERA LEUCOTRICHA (ELL. & EV.) SALM.

By F. R. Petherbridge, M.A. and W. A. R. Dillon Weston, M.A., School of Agriculture, Cambridge.

In his paper on "Studies on *Podosphaera leucotricha*" Woodward (*Trans. Brit. Mycol. Soc.* xii, 1927, pp. 195–196) states that "The mildew apparent at bud-break is derived from hibernating mycelia established there during a previous season, and is rarely, if ever, due to infection from outside sources. The presence of mildew in spring, then, is dependent entirely upon the existence of infected buds and the number and distribution of these buds determine the severity of attack....The evidence is entirely opposed to the possibility of the spread of the disease by 'Secondary infection'....What appeared remarkable was that buds which did not harbour the fungus, although situated between infected buds on an infected twig, opened and remained entirely free from Mildew throughout the summer."*

This does not agree with our observations on "secondary infection" as we were already in possession of figures which we regarded as evidence of this on some Chivers Seedling apples near Cambridge. On April 6th, 1924, we cut out all the obviously mildewed trusses but later in the season we noticed that quite a number of the leaves still showed the presence of mildew.

In 1927 counts were made of the mildewed trusses on some Chivers Seedling apples (nine years old) during the fourth week in April and during the first week in July. The figures obtained are given in the following table and show a marked increase in the number of mildewed trusses.

* Woodward (in lit.): "This extract is misleading and the whole of pp. 195–6 of my paper should be read."

Plot	Number of trusses examined	Percentage of mildewed trusses	Date examined
II	3200	13	4th week in April
	510	68	1st „ July
IX	1000	21	4th „ April
	498	63	1st „ July
XIV	1000	15	4th „ April
	505	67	1st „ July
XV	1000	15	4th „ April
	571	57	1st „ July

The figures were obtained by taking a number of trusses at random on about twenty trees in each plot and counting those which were obviously mildewed. The trusses were not carefully examined for slight attacks.

In 1928 we decided to label a number of healthy trusses when the primary infected ones were very apparent.

On April 18th and 23rd a number of healthy trusses—chiefly shoot trusses—were labelled with red raffia. Five days later these trusses were examined but no signs of mildew found. On May 17th an examination of two hundred and thirty-three of the labelled trusses showed that one hundred and eighty-six of them (*i.e.* 80 per cent.) were attacked by mildew. Many of the trusses that were apparently healthy were found on careful examination to be slightly attacked.

On May 24th an examination of one hundred and four labelled trusses showed only three trusses entirely free from mildew. On that date we also examined one hundred trusses which appeared to be clean (that is they showed no primary infections or obvious mildewed appearance). On closer examination, however, ninety-four showed the presence of mildew. (The six clean shoots were fruit trusses.) We then examined fifty shoot trusses and fifty fruit trusses that were apparently clean, but on more detailed examination, the fifty shoot trusses were seen to be mildewed as were forty of the fruit trusses.

On April 23rd we artificially contaminated sixty-four clean trusses on two trees with spores from a mildewed shoot. This was done by moistening the trusses with water and then dusting them with spores from a mildewed shoot. On May 17th sixty of these trusses were attacked by mildew.

Nature of secondary infection.

These secondary infections were very easy to distinguish from the primary infections. At this stage (April 23rd) most of the primary infected trusses were mildewed all over and had taken on a dirty looking appearance, whereas in the secondary infected trusses only a small portion of the truss was attacked at

this stage and the mildewed portion showed as white patches, as do the primary infected trusses in the early stages. In many of the secondary infections only a small patch of mildew was found, sometimes near the midrib, and sometimes near the edge of the leaf. The slight curling of the leaf was helpful in finding the infected trusses.

There is very little likelihood that the trusses which we labelled were artificially infected by us as we did not handle any of the primary infected shoots. These trees are particularly interesting as they had the worst attack of mildew that we have ever seen.

On May 24th a very large percentage of the wood trusses showed signs of mildew attack whereas when examined on April 23rd most of them were free from attack. Even at this date a number of the trusses had to be very carefully examined in order to find the mildew.

On June 5th we examined some Bramleys Seedling trees near Lakenheath and found that a very large percentage of the shoot trusses were slightly attacked by mildew. These trusses were similar in appearance to the "secondary infected" trusses on the Chivers Seedling trees and were easily distinguished from primary infected trusses.

The above provides abundant evidence that in the varieties Chivers Seedling and Bramleys Seedling "secondary infection" may be an important factor in the spread of this disease, and our observations in fruit plantations supports the view that this is true of certain other varieties.

OBSERVATIONS ON THE BACTERIAL AND FUNGAL FLORA OF THE UPPER AIR.

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THIS paper records some work that was carried out in spore-trapping experiments from airplanes. The flights were made from Duxford in machines belonging to the Cambridge University Air Squadron. The work was started at the end of 1926 and since that date various types of spore-trap have been used. The simplest method employed was to expose in the air microscope slides (3 inches by 1 inch) smeared with vaseline; these were exposed by hand from the cockpit. Another method, but more difficult in operating, was by means of photographic slide cases fixed in a brass clamp on the upper wing above the cockpit. Each case contained two quarter plates smeared with vaseline

and the exposure was made by withdrawing the slide of the case for a given time; the reverse side of the case contained a similar plate which acted as a control. A somewhat similar method consisted in exposing the same type of photographic slide cases by hand from the cockpit. Another method which was tried was by exposing slides in a mechanical spore-trap attached to the end of the wing; this was very similar to that described by Stakman, Henry, Curran and Christopher*. It was operated in the same way from the cockpit.

When the slide cases were taken to the laboratory they were opened quickly and the plates immediately covered with large cover slips. These different types of spore-traps were operated by Mr Everett of the Hampshire Light Aero Club and Lieut. Goddard of the Cambridge University Air Squadron. The objections to the above methods, in my opinion, are these: the chance that the slide may become contaminated when applying the vaseline, the difficulty of insuring that the interiors of the slide cases are not contaminated before and after exposure, the risk of contaminating the slides when placing on the cover slips and lastly the difficulty of identifying the spore so obtained. Where a few spores only are obtained on a plate there is always the just criticism to be met that these slides were contaminated prior to or after exposure. On this account I abandoned these methods and decided not to communicate the results obtained. The trend of these experiments showed, however, that the upper air contained a large quantity of spores. *En passant* I consider one of the best methods yet adopted to be that of Stakman, Henry, Gordon, and Christopher who place inside a bottle a microscope slide attached to a wooden paddle, the upper part of which extends through a hole in the cork of the bottle and serves as a handle, after exposure the slide is again placed in the bottle. Unfortunately, as these authors state, the method is very cumbersome.

The method I finally adopted was to expose culture media in (*a*) test tubes, (*b*) Petri dishes. The exposures were made at the altitude required and then sealed and at a later date examined for contaminations. For the very general observations that were made this method was serviceable. In one flight an exhausted flask containing potato agar was taken up with the intention of exposing it above 10,000 feet; since, however, this altitude was not reached the flask was not exposed and was taken back to the laboratory. During the night the flask burst (or collapsed) with some violence. It is possible that such a method would involve some risk since the glass would be subject to changing stresses.

* Spores in the Upper Air. Journ. Agric. Res. xxiv.

Table I shows the results of a series of flights which were carried out from Duxford Aerodrome and in which test tubes containing potato agar were exposed at various altitudes.

This table shows that approximately forty per cent. of the exposures were positive and illustrates the ubiquitous nature of microscopic plant life, and shows what an excellent medium the air must be for the dissemination of pathogenic and saprophytic organisms.

Table II shows the results that were obtained on exposing Petri dishes containing potato agar.

The figures in this table show that spores and bacteria may be found at very great heights and yet still retain their vitality. It is interesting to note that in the flight on January 31st, 1928, the last dishes exposed at 9000 and 10,000 feet showed only bacterial colonies and that no fungi developed. It is very probable that bacteria and the lighter spores may be carried to much greater heights than this, and it seems reasonable to anticipate that in this rarer atmosphere the last living organisms would be bacteria.

A just criticism of these experiments would be that the plates when exposed, picked up spores attached to the airplane, which were released by the slip stream. This is a distinct possibility but any serious contamination appears unlikely for these reasons. The plates were held at arm's length from the cockpit and the plate faced between the struts so that it was approximately between the upper and lower wings. Again, the negative nature of the exposures at 13,000 feet is evidence itself against any serious contamination of this nature. In this last connection it is interesting to note that Stakman, Henry, Curran, and Christopher have obtained spores at a height as great as 16,500 feet. They state that "The highest altitude at which slides were exposed was 16,500 feet or more than 3 miles above the surface of the earth. This slide was exposed between Waco and San Antonio, Tex. on April 28th, 1921, and two urediniospores of what appeared to be *Puccinia triticina* were caught. It would not be safe, however, to conclude that spores normally occur at this height, as only a few flights were made at such extreme elevations. Spores are very numerous up to about 11,000 feet but at higher altitude they apparently are relatively scarce."

In Table III are given the results obtained when Petri dishes containing potato agar were exposed below, in, and above the clouds.

This table shows that in these flights there was a higher bacterial and fungal flora in the clouds than above or below them. It is probable that spores may form surfaces for condensation of water vapour. It would be anticipated that there

would be a higher bacterial and fungal flora in clouds than immediately above or below them. In considering Table III the relative heights at which the exposures were made should also be taken into account. Generally speaking the nearer the earth the higher will be the bacterial and fungal flora. For example, in the flight made on May 29th, 1928, a plate exposed for one minute at 1500 feet (not quoted in the table) showed after seven days the presence of thirty-five fungi and sixty-two bacterial colonies.

Table I.

Date	Altitude (in ft.) at which exposures were made	Time of exposure in seconds	Negative (N) or positive (P) after 7 days	Negative (N) or positive (P) after 21 days
14. x. 27	1,000	30	—	N
	1,000	30	—	N
	1,000	30	—	N
17. x. 27	1,000	30	—	N
	1,500	30	—	N
	2,000	30	—	P
	3,000	30	—	N
	4,000	30	—	N
	5,000	30	—	N
	5,500	30	—	P
	6,000	30	—	P
	6,000	30	—	N
	6,000	30	—	N
26. x. 27	1,000–1,500	30	—	N
	1,000–1,500	30	—	P
	1,000–1,500	30	—	P
	1,000	30	—	P
	1,500	30	—	N
	2,000	30	—	P
	2,500	30	—	N
	2,500	30	—	N
	2,500	30	—	N
4. xi. 27	500	30	—	P
	600	30	—	P
	600	30	—	P
	600	30	—	N
	700	30	—	P
	700	30	—	P
	800	30	—	P
	800	30	—	P
	900	30	—	N
	900	30	—	N
7. xi. 27	2,000	30	—	P
	2,000	30	—	N
	2,000	30	—	N
	2,000	30	—	P
	2,000	30	—	P
	2,000	30	—	P
	1,500	30	—	N
	1,500	30	—	P
	1,700	30	—	N
	1,800	30	—	N

Table I (*cont.*)

Date	Altitude (in ft.) at which exposures were made	Time of exposure in seconds	Negative (N) or positive (P) after 7 days	Negative (N) or positive (P) after 21 days
17. i. 28	3,500	30	P	P
	5,000	30	N	N
	6,500	30	N	P
	7,500	60	N	P
	8,500	60	N	N
	10,000	300	N	N
31. i. 28	1,000–1,200	60	P	—
	3,000	60	N	—
	5,000	60	N	—
	6,500–7,000	60	N	—
	8,000–8,500	60	N	—
	9,000	60	N	—
	9,500	60	N	—
	10,000	60	N	—
	10,000	60	N	—
	11,000	60	N	—
2. ii. 28	1,000–2,000	60	N	—
	2,000–3,000	60	P	—
	3,000–4,000	60	N	—
	4,500–5,000	60	N	—
	5,000–5,500	60	P	—

An interesting flight was made from Duxford to Cambridge at an altitude of 2000 feet on May 20th; the sky was cloudless. Three plates were exposed for a period of one minute. On arrival at Cambridge the machine was put up to 4000 feet and the return journey made, three exposures being taken. A seventh plate was exposed as the machine was descending from 4000 feet to the aerodrome. After five days these Petri dishes were examined but it was impossible to count the number of contaminations on the dishes exposed on the outward journey. The dishes were literally covered with bacterial and fungal growths and many hundreds of spores and bacteria must have alighted on the medium. The same was true of the Petri dish exposed in descending from 4000 feet to the aerodrome. The plates exposed on the return journey at 4000 feet were much less heavily contaminated but these contaminations were greater than those obtained in previous flights.

If this flight be compared with those made in the winter months it is clear that in summer—or at least at the end of May—the air is very much more heavily charged with bacterial and fungal spores. The results obtained from these exposures render it easy to visualise how local epidemics of plant and animal diseases may be brought about.

Table II.

Date	Altitude	No. of mycelial growths which developed after 7 days	No. of bacterial colonies which developed after 7 days*	Time of exposure in seconds
31. i. 28	2,000	10	3	60
	4,000	7	11	60
	6,000	3	2	60
	8,000	1	0	60
	9,500	0	9	60
	10,500	0	6	60
2. ii. 28	1,000	14 (15)†	13 (25)†	30
	2,000	3 (3)	5 (5)	30
	3,000	4 (8)	8 (8)	30
	4,500	6 (6)	3 (3)	30
	6,000	0 (1)	1 (1)	30
	7,000	2 (3)	4 (5)	30
9. ii. 28	500	11	12	30
	500	7	5	30
	1,000	7	15	30
	1,500	14	15	30
	2,000	11	3	30
	2,000	5	5	30
	2,000	1	2	30
	2,500	3	7	30
	2,500	6	8	30
	2,500	8	6	30
	2,500	11	6	30
	2,500	3	5	30
22. ii. 28	2,000	7	7	30
	4,000	3	14	30
	6,000	6	7	30
	8,000	0	0	30
	9,000	2	1	30
	10,000	0	1	30
	12,000	3	1	30
	13,000	0	0	30
	13,000	0	0	30
	13,000	0	0	30

† Same plates examined after 14 days.

Discussion of Results.

The results show the ubiquitous nature of fungal spores and bacteria in the upper air and that a large number of these are viable even at an altitude of two miles above the earth. From the flights made it would seem clear that in the summer (as one would expect) the air is very much more heavily charged with fungal spores and bacteria than in the winter months. The trend of the work suggests that the air is the ideal medium for the

* I have since received a report from Mr H. J. Barker who kindly investigated some of these bateria. In a short summary of his results he states:—
"Nearly all the organisms are coloured types. This is usual in samples from the air. Of the twenty types isolated, eleven were bacteria (=non-sporing rods), two were bacilli (=sporing rods), four were cocci (including one sarcina), and three were Actinomycetes."

transportation of microscopic organisms and suggests that epidemics of plant and animal diseases may be brought about in this manner. ("It seems clear that there is a relationship between clouds or eddies of spores and localised heavy field infections of 'rust'":—Report of the Dominion Botanist for Canada, 1926, pp. 111.)

Table III.

Date	Altitude at which exposure was made	How exposed	Time of exposure in secs.	No. of fungi developing after 7 days	No. of bacterial colonies developing after 7 days	Remarks
7. iii. 28	2000	Exposed in slight drift of clouds	30	8	3	In clouds
	2000	,,	30	2	0	Bacterial
	4000	In clear air	30	0	0	Fungi colonies
	4400	In cloud bank	30	3	0	14 3
	4500	,,	30	1	0	Below or above
	4700	Above this cloud bank	30	0	0	clouds
	4800	,,	30	0	0	0 0
29. v. 28	3000	Below cloud	30	7	2	In clouds
	3000	,,	30	5	5	
	4500	In cloud	30	3	7	Bacterial
	4000	Below cloud	30	7	2	Fungi colonies
	3000	,,	30	16	5	60 64
	4000	In cloud	30	16	25	
	3500	Below cloud	30	10	1	Below cloud
	4000	In cloud	30	22	23	
	4000	,,	30	8	3	45 15
	4000	,,	30	11	9	

Some evidence has also been obtained that the clouds are more heavily charged with fungal spores and bacteria than the air a little below them. This is likely since spores would form suitable surfaces for the condensation of water vapour.

In one flight three plates were exposed at 13,000 feet and no development of fungi or bacteria took place. It is very probable, however, that viable organisms are to be met with considerably higher than this. The trend of the work suggests that at 10,000 feet the air is relatively free from microscopic organisms.

In conclusion the writer wishes to express his thanks to Group Captain Bowen, late Wing Commander of the Cambridge University Air Squadron, for his kindness and interest in the work and to Flight Lieutenant Goddard who has assisted him in ways too numerous to mention and from whom he has at all times received unqualified assistance. He also records his thanks to the Flight Instructors, Lieuts. French, Hordern and Nash, and finally to Mr Everett who co-operated in the first part of the work and carried out some of the experiments with various types of spore-traps.

A COMPARATIVE MORPHOLOGICAL AND PHYSIOLOGICAL STUDY OF A NUMBER OF STRAINS OF BOTRYTIS CINEREA PERS. WITH SPECIAL REFERENCE TO THEIR VIRULENCE.

By W. R. C. Paul, B.A., B.Sc.

(With Seven Tables, Two Text-figures and Plate II.)

Introduction.

The aim of this investigation was in the first instance to carry out a comparative study of a number of strains of *Botrytis cinerea* from the purely morphological standpoint in order to obtain some idea of the limits of variability of the different forms. It was then proposed to examine the parasitic activity of a selected number of strains on a fairly wide range of host plants to determine whether particular strains were generally more virulent than others, or alternatively whether some degree of selective parasitism was shown. Lastly, when it was found that some strains were more actively parasitic than others, an attempt was made to correlate the different degrees of parasitism shown with certain physiological features of the various strains.

Preliminary Experiments.

A preliminary examination was made of a number of cultures of *Botrytis cinerea* Pers. which were kept among the stock cultures in the Plant Pathological Laboratory of the Imperial College of Science. The majority of these had been isolated from various diseased plants in the course of student work. The following is a list of all the cultures which were tested, together with a statement of their mode of origin:

	Source
A. Isolated from diseased *Geranium* leaves	Chelsea Physic Garden
B. Isolated from diseased *Chrysanthemum* leaves	,,
C. A saltant strain from the *Chrysanthemum* culture	
D. Isolated from diseased Hyacinth bulbs	,,
E. Isolated from diseased Tomato fruit	Purchased at a shop
F. Culture received from Dr J. Westerdijk	Amsterdam

At an early stage of the work, the purity of the cultures was ensured by the method of single hyphal tip isolations as described by Brown (5). Stock cultures were made on potato-

extract agar slopes and after incubation for two weeks at 21° C. kept under ordinary laboratory conditions. They were renewed at intervals of six weeks. Reculturing was done on potato-mush agar slopes from which transfers were made at fairly frequent intervals and used as the source of inoculum for subsequent experimental work. The culture C mentioned above as a saltant strain from the *Chrysanthemum* culture cannot be guaranteed as such, since it appeared in the course of certain preliminary work before the various cultures had been subjected to purification by the hyphal tip method. This strain appeared on a plate culture as a definite sector which was clearly marked off from the rest of the colony. The new strain showed certain well-defined characteristics and was therefore used to a considerable extent in the comparative study which was subsequently carried out.

A general comparison of the various forms was made on plate cultures of potato-extract agar. An inoculum of spores and mycelium was placed near the centre of each plate and then incubated at 21° C. for two weeks. The cultures were examined at the end of this period, when they showed the following features:

A. Conidia formed evenly over the whole surface; sclerotia absent; very little aerial mycelium.
B. Conidia formed in localised areas between sclerotial areas; sclerotia in the centre of the plate and in a zone at a short distance from the centre; a few sclerotia outside this zone in the form of rays extending towards the periphery; little aerial mycelium.
C. Very similar to A.
D. Conidia formed at the centre and periphery; sclerotia absent; aerial mycelium formed abundantly over the rest of the surface.
E. Very similar to A.
F. Conidia formed in localised areas; a large sclerotium in centre and others scattered irregularly over the surface.

The forms A, C and E were thus of a highly sporing type. A and E were not definitely distinguishable from each other, but C (the saltant) differed from the other two in its shorter and more compact conidiophores. Forms B and F were clearly sclerotial types, and D a predominantly mycelial type.

There are thus distinguishable three types of strains: (1) a sclerotial type; (2) a mycelial type, and (3) a sporing type. In the main therefore the work was simplified by selecting one strain of each type as follows:

1. Dr Westerdijk's strain—sclerotial type.
2. Strain from Hyacinth—mycelial type.
3. Saltant strain—sporing type.

For convenience in description these will be referred to as *Sc, M* and *Sp* respectively.

CULTURAL FEATURES OF STRAINS ON A VARIETY OF MEDIA.

(1) *General cultural appearance.* For purposes of this general comparison the strains were grown on three synthetic media:

(*a*) Glucose-starch-peptone medium:

Glucose	15 gm.	$MgSO_4$	0·75 gm.
Potato starch	20 gm.	Agar	15 gm.
Peptone	5 gm.	Water	1 litre
K_2HPO_4	1·25 gm.		

(*b*) Glucose-starch-asparagin medium:

Glucose	2 gm.	$MgSO_4$	0·75 gm.
Starch	10 gm.	Agar	15 gm.
Asparagin	2 gm.	Water	1 litre
K_3PO_4	1·25 gm.		

(*c*) Coon's medium:

Maltose	7 gm.	$MgSO_4$	1·2 gm.
Asparagin	2 gm.	Agar	15 gm.
KH_2PO_4	2·7 gm.	Water	1 litre

and on potato-mush agar, prune-juice agar and turnip-extract agar. The cultures were set up both in Petri dishes and as slants in test tubes.

From subsidiary experiments it was found that no material difference appeared in the cultures whether the inocula used were composed of spores only or of aerial mycelium only. Hence the inoculum generally used was a small mass of mycelium and spores which was placed near the centre of the plate. The inocula were always taken from cultures on slopes of potato-mush agar which had been incubated for two weeks at 21° C.

Table I gives a general comparison of the relative development of aerial mycelium, sclerotia and spores by the three types of strain on the different media. The last are arranged in the table roughly in descending order of concentration. The data refer to cultures grown in an incubator at 21° C. and which were two to three weeks old.

It is clear that strain *Sc* shows the sclerotium-forming character on all media except the weakest ones, and that this feature is more marked in this strain than in the other two. Strain *M* on the other hand tends to form profuse aerial mycelium, and this feature is most prominent in media of intermediate concentration. Strain *Sp* is a form which has a minimal tendency to the formation of aerial mycelium; it shows sclerotial development on most of the stronger media, and on all media tested produces abundant sporulation. Thus while the prominence of the various features can be modified by choice of medium, it is nevertheless true that the various strains show marked tendencies in certain directions over a wide range of

media. Strain *Sc* may be described generally as sclerotium-forming, *M* as aerial-mycelium-forming, and *Sp* as spore-forming.

Table I. *Comparative development of the three strains on different media.*

Medium	Strain	Aerial mycelium	Sclerotial production	Sporulation
Glucose-starch-peptone agar	*Sc*	+	+++	−
	M	++	+	+
	Sp	−	−	++
Potato-mush agar	*Sc*	+	+++	++
	M	++	+	++
	Sp	−	+	+++
Glucose-starch-asparagin agar	*Sc*	++	+++	+
	M	+++	−	+
	Sp	−	+	++
Prune-juice agar	*Sc*	++	++	−
	M	+++	−	−
	Sp	−	−	++
Turnip-extract agar	*Sc*	+	−	+
	M	++	−	+
	Sp	−	−	++
Coon's agar	*Sc*	+	−	−
	M	++	−	+
	Sp	−	−	++

+++ abundant; ++ moderate; + weak; − absent.

As shown in Table I, the sclerotial strain *Sc* forms abundant sclerotia and also sporulates moderately on potato-mush agar. This refers to growth of colonies at 21° C. Lowering of the temperature increases sclerotial formation and reduces sporulation. Thus at 12° C. this strain produces a white felt-like growth with very numerous sclerotia and with no spores. When on the other hand the colonies are grown at a temperature of 27° C. growth is retarded, and neither sclerotia nor spores are formed. This high temperature however does not inhibit the sporulation of Strain *Sp*.

A further series of cultural differences observed was as follows:

The sclerotia produced by strain *Sc* appear earlier than those in the other two strains, and some of them reach a much greater size (16 × 7 mm. as against 2 × 3 mm.).

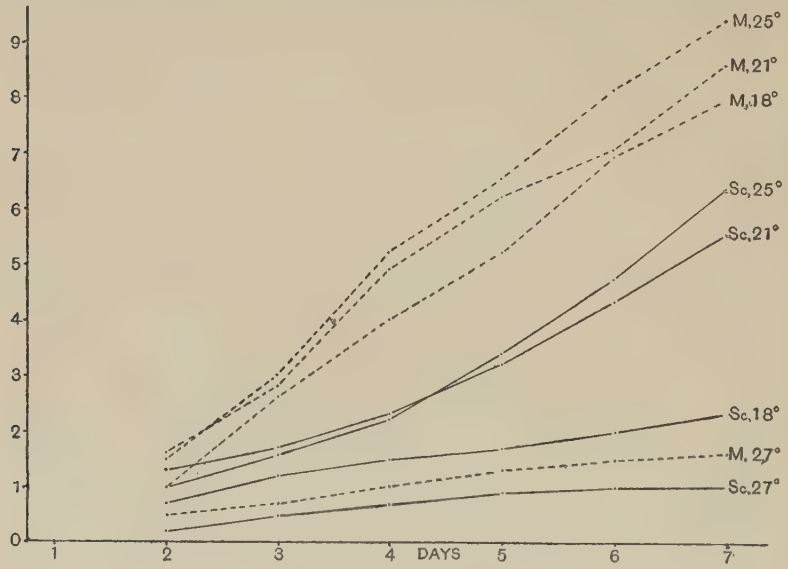
The tendency to form attachment organs when the fungus comes in contact with the glass of the Petri dish is much greater in the mycelial strain (*M*) than in the others.

On the stronger media strains *Sc* and *M* show pronounced corrugation of the surface of the medium due to intercalary growth in the thick superficial skin or plectenchyma. This

feature is especially well seen in strain *Sc*. No such corrugation of the surface occurs in any culture of the strain *Sp*.

The appearance of typical plate cultures of the three strains on potato-mush agar, on glucose-starch-peptone agar and on glucose-starch-asparagin agar is illustrated in Pl. II, figs. 1–7.

The general appearances shown by the cultures grown as slopes in test tubes are very similar to those just described. The most striking difference observed is the tendency of the slope cultures to produce aerial mycelium at the upper ex-



Text-fig. 1. Showing rates of growth of strains *Sc* and *M* on potato-extract agar at different temperatures.

tremity of the slope. Even the strain *Sp* generally shows some aerial mycelium at the upper end of a slope culture, though plate cultures of this strain rarely produce any obvious aerial mycelium.

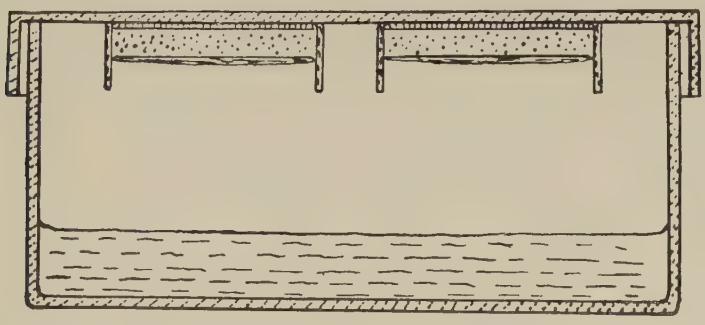
(2) *Comparison of growth rates*. Comparative studies of the rates of colony growth were made at various temperatures and on a number of media for the three strains *Sc*, *M*, and *Sp*. On all the media except Coon's agar, strains *M* and *Sp* showed very similar growth rates, while strain *Sc* grew much more slowly. The rates of growth of strains *Sc* and *M* on potato-extract agar are plotted in Text-fig. 1 for a number of temperatures.

The optimum temperature for growth appears to be very similar for the three strains, viz. between 21° C. and 25° C., and probably nearer the latter temperature. It may be noted

that the growth rate always falls off very rapidly even a few degrees above the optimum temperature.

(3) *Effect of environmental conditions on cultural features.* This has already been dealt with to some extent in Table I, where the influence of the cultural medium on the type of growth produced has been stated. There remains to describe the effect of certain physical factors, such as varying atmospheric humidity and illumination. The manner in which the plates are inoculated in the first instance also exerts an influence on the subsequent growth.

In the series of experiments relating to the effect of *humidity* on growth, two strains of *Botrytis cinerea* were used, one the strain *Sc* already mentioned and the other a strongly sporing



Text-fig. 2. Illustrating methods of exposing cultures during growth to atmospheres of different humidities.

strain (*Sp'*) isolated from tomato fruit. The cultural medium used was potato-mush agar, containing 200 gm. of fresh potato to the litre.

The method of exposing the fungal cultures to atmospheres of different degrees of humidity was as follows. The Petri dishes (7 cm. diam.) in which the fungus was growing were fixed by means of gelatine solution to the lids of large glass dishes (ca. 20–25 cm. diam.) and then set up in the manner indicated in Text-fig. 2. In the bottoms of the large dishes were placed solutions of different vapour pressures. In general, four Petri dishes were affixed to the lid of each container so that a comparison in duplicate of the behaviour of the two strains could be made. The liquid placed in the bottom (200 c.c.) was either water or a sulphuric acid-water mixture (10, 20, 30 volume per cent. H_2SO_4).

It is not possible to state the actual relative humidity prevailing over the growing cultures. Obviously the experimental arrangement is not a static one, so that when a drying liquid

is placed in the bottom, a continuous passage of water vapour will take place from the Petri dishes to the underlying drying liquid. There will be a gradient of humidity from the neighbourhood of the growing cultures to the liquid. Thus the degree of humidity in which the cultures grow is not identical with that prevailing over the underlying liquid, which can be readily determined from tables. However, while the actual humidity prevailing cannot be stated, it is clear that the above experimental method allows of a range of humidities being set up in a perfectly definite manner. It is essential that the details should be standardised, and in particular that the large dishes used should all be of the same dimensions, especially as regards depth.

Table II gives a comparison of strains *Sc* and *Sp'* in atmospheres of three degrees of humidity. The cultures were inoculated at the centre with a small mass of spores and mycelium. The records refer to the appearances of the various cultures after sixteen days' growth at laboratory temperature.

Table II. *Showing effect of varying atmospheric humidity on growth-form of strains.*

Moisture concentration	Strain *Sc*	Strain *Sp'*
Over water	*Mycelium:* in white silky festoons, hanging down to water	*Mycelium:* as in *Sc* but not so profuse
	Spores: few or none	*Spores:* few
	Sclerotia: large and numerous, chiefly central	*Sclerotia:* small, numerous and scattered
Over 10 % H_2SO_4	*Mycelium:* hanging down in white festoons, but not extending so far as when over water	*Mycelium:* white silky strands only near edge of Petri dishes
	Spores: few	*Spores:* fairly abundant
	Sclerotia: present in fair abundance beneath mycelium	*Sclerotia:* only one or two present
Over 20 % H_2SO_4	*Mycelium:* confined to edge of dishes	*Mycelium:* no aerial mycelium apart from conidiophores
	Spores: fairly abundant over the greater part of surface	*Spores:* intense formation over whole surface
	Sclerotia: only a few	*Sclerotia:* none

The table shows clearly the effect of humidity on spore formation. When strain *Sp'* is grown in a drying atmosphere, such as is obtained over 20 per cent. H_2SO_4, it produces an intense crop of spores on relatively short conidiophores. When, on the other hand, it is grown in an atmosphere which is as nearly as possible saturated with water vapour, the aerial mycelium, which in a drying atmosphere remains short, continues to grow more or less indefinitely, forming long pendent

festoons. Under these conditions practically no spores are formed. Humidity conditions which favour sporulation tend to inhibit sclerotium formation and *vice versa*.

The effect of the humidity factor is the same in both strains examined. Under conditions of high humidity both show strong sclerotial production and feeble sporulation; whereas under much drier conditions, both may show heavy sporulation and feeble sclerotial formation. Under intermediate conditions of humidity, strain *Sc* may show in the main sclerotium formation only, while strain *Sp'* under the same conditions is of the sporulating type. It is clear therefore that the difference between the two strains is essentially only one of degree.

The inverse correlation between spore formation and sclerotium formation has been indicated above. This inverse correlation does not however apply under all circumstances. Thus, dilution of the nutrient medium results in more limited sporulation and also in the production of fewer and smaller sclerotia. One may say therefore that, within the limits of strength of nutrient examined, the amount of spore formation or of sclerotium formation increases with the vigour of growth, and that under any given set of nutritive conditions, the extent to which growth proceeds in the direction of sclerotia or of spores is controlled chiefly by the prevailing conditions of humidity.

The formative effect of *light* was tested on strains of the sclerotial and sporing type, the media employed being a series of dilutions of potato-mush agar. One series of plates was wrapped up in black paper; a similar series which was placed alongside was subject to the normal alternation of day and night. Both series were placed on the laboratory table in diffused light.

The general result of the comparison was as follows:

Sclerotia. These increase in number with the concentration of the medium, and are formed more freely in the dark than in the light over the whole range of concentrations. In the more concentrated media used, the sclerotia formed in the dark are much larger than those formed in the light.

Spores. These are formed more freely in the light than in the dark. When the sporing type of strain is grown on concentrated media the spores are confined almost entirely to the margin of the plate when this is kept in the dark, whereas in the light sporulation is fairly general over the whole surface. At the lower concentrations of medium, little difference is apparent between the amount of sporulation in the light and in the dark.

The general trend of the effect of illumination on growth-form is the same for both types of strain. The difference between them is again one of degree only. It should be pointed out,

however, that the experimental method adopted in the preceding tests on the effect of light is not sufficiently critical, in that the darkened plates would be almost certainly under conditions of higher humidity than the illuminated controls. The effects observed may therefore be due in part to altered humidity conditions.

The effect of the manner of inoculation upon growth-form was tested by comparing a series of cultures in which the inoculum was placed in a spot at the centre of the plate with another in which the fungal spores were uniformly distributed throughout the medium before pouring. The experiment was carried out over a range of humidity conditions and with the two strains *Sc* and *Sp'*.

When the atmosphere is saturated, the amount of sporulation is negligible, and apart from a slight difference in arrangement, the sclerotia are not affected. When however conditions of humidity are such as to allow of sporulation, this is greater and sclerotium formation is less in the plates where the inoculum has been uniformly distributed than in the corresponding plates which were inoculated at a single spot. As might be anticipated, this effect due to the manner of inoculation is most clearly shown under conditions of fairly high humidity in the strongly sporing strain, and under conditions of low humidity in the sclerotial strain. When, for example, humidity is low the sporulation of the sporing strain is always so intense that differences in amount cannot be detected.

It is clear therefore that while the different types of strain show certain general tendencies in their growth-forms, nevertheless considerable modification is possible as a result of the interplay of environmental conditions.

(4) *Variation in spore size.* Apart from the macroscopic differences already described, a definite variation in spore size could be established between certain strains. The mean length and width of spores of strains *Sc*, *M* and *Sp* as obtained from measurements of one hundred spores of each taken from cultures on potato-mush agar (temp. 21° C.) are as below:

Strain	Length	Width
Sc	11·4 μ	8·9 μ
M	11·0 μ	8·8 μ
Sp	10·5 μ	6·1 μ

As regards mean length no distinct difference is to be noted, and strains *Sc* and *M* have the same spore width. Strain *Sp*, however, produces a distinctly narrower spore. As the mean spore length is approximately the same for all three strains, it follows that the spores of strain *Sp* are more elliptical in outline than those of the other two.

(5) *Rate of starch hydrolysis.* A starch-agar medium of the following composition was prepared:

Potato starch	20 gm.	$MgSO_4$	0·75 gm.
Asparagin	2 gm.	Agar	20 gm.
K_2PO_4	1·25 gm.	Water	1 litre

Plates of this medium were inoculated at the centre with strains *Sc*, *M* and *Sp* and incubated for nine days at 25° C. At the end of this period the diameters of the colonies were: strain *Sc*, 5·1 cm.; strain *M*, 7·9 cm.; strain *Sp*, 7·1 cm. Strain *Sc* as usual grew most slowly. When the plates were irrigated with iodine solution to test the amount of starch hydrolysis which had taken place, it was found that the diameters of the areas cleared of starch were: strain *Sc*, 1·6 cm.; strain *M*, 4·3 cm.; strain *Sp*, 1·1 cm. The smallness of the starch-free area in strain *Sc* is partly discounted by the slow rate of spread of this strain. This explanation however does not apply to strain *Sp*, the rate of spread of which is almost as great as that of strain *M*, though the amount of starch hydrolysis is much less. Strain *Sp* therefore appears to possess much smaller amylolytic activity than is shown by strain *M*. This difference is probably correlated with the greater development of vegetative mycelium by the latter strain.

Parasitic behaviour of strains on a number of hosts.

Comparative tests were carried out on apple fruit, and on leaves of broad bean, *Eucharis Mastersi*, lilac, lily of the valley, hyacinth, and various species of *Begonia*. As far as possible the comparisons were made in a quantitative manner.

The apples (Newtown Pippins) were inoculated according to the method described by Granger and Horne (8). The experiments with leaves were carried out by laying the spore suspensions on the uninjured surface (*e.g.* broad bean, lilac) but more generally, the surface was wounded, either by shaving with a razor or pricking with a needle. In a few cases the spore suspension was injected into the intercellular spaces of the leaf by means of a hypodermic syringe. Controls were set up in the usual manner. The inocula consisted of suspensions of spores in a weak turnip extract. In order that approximately the same number of spores should be put on for each strain, a measured volume of spores (as obtained by centrifuging) was suspended in a definite volume of nutrient liquid. This precaution is however to a large extent unnecessary, as it was known from subsidiary experiments that the rate of advance of attack is, within wide limits, independent of the concentration of spores present in the inoculum.

In the experiments with leaves, the amount of attack was

expressed in terms of the average linear dimensions of the invaded area; with the apple fruit, the weight of rotted tissue was determined.

Table III gives the results of the series of experiments carried out in this connection. In columns 4, 5 and 6 are set out the mean amounts of attack, together with the probable error of each of these mean values. Column 3 gives the period during which attack has proceeded. The method of inoculation is indicated in column 1, whether on unwounded (unw.) or wounded (w.) tissue or by injection (inj.). The experiments were carried out either at laboratory temperature or in a 21° incubator.

Table III. *Illustrating the different degree of virulence of three strains.*

Host	No. tested for each strain	Duration (days)	*Sc*	*M*	*Sp*
Apple fruit (w.)	14	14	2·9 ± 0·2 gm.	81·6 ± 2·7 gm.	4·9 ± 0·52 gm.
Bean leaf (unw.)	20	7	0·46 ± 0·026 cm.	1·98 ± 0·08 cm.	1·16 ± 0·04 cm.
,, (inj.)	20	7	0·58 ± 0·033	2·50 ± 0·1	1·41 ± 0·08
Eucharis Mastersi (w.)	8	7	0·25 ± 0·017	1·3 ± 0·06	0·51 ± 0·018
Begonia Haageana (w.)	5	7	1·55 ± 0·07	4·25 ± 0·12	2·1 ± 0·06
B. heraclaefolia (w.)	5	7	0·85 ± 0·085	4·28 ± 0·07	2·4 ± 0·134
B. semperflorens (w.)	12	7	1·38 ± 0·065	3·93 ± 0·1	2·25 ± 0·075
B. argenteo-guttata (w.)	5	7	1·52 ± 0·13	5·56 ± 0·12	2·52 ± 0·08
Lilac (unw.)	12	7	Nil	2·4 ± 0·06	0·87 ± 0·04
,, (w.)	12	7	0·57 ± 0·016	3·22 ± 0·07	1·06 ± 0·06
Lily of the Valley (w.)	10	7	0·95 ± 0·04	3·62 ± 0·11	1·64 ± 0·06

In all the experiments *M* is the most actively parasitic strain, *Sc* is the weakest and *Sp* is intermediate. A similar result was indicated in the tests with hyacinth leaves. With these however the areas which were attacked were not sharply marked off from those which were healthy, so that a quantitative statement of the differences is not possible.

The different rates of attack of the three strains on lilac leaves are illustrated in Pl. II, fig. 8.

In preparing Table IV, the differences (indicated by *M–Sc*, *M–Sp*, *Sp–Sc*) have been determined. The figures in the table give the number of times these differences exceed the corresponding probable errors. As a difference which is three times the probable error is reckoned as significant, it is clear that the results in Table IV are statistically significant in a very high degree.

The results which are summarised in Table III and the degree of significance of which is shown in Table IV prove that over a wide range of host tissues the strain *M* is uniformly the most actively parasitic, that strain *Sp* is of intermediate virulence and that strain *Sc* is the least active of the three. No evidence

of selective action on the part of any of the three strains has been met with, that is, the relative order of parasitic vigour has been the same on all the hosts tested.

Table IV. *Illustrating the significance of the differences in parasitic vigour shown in Table III.*

Host	*M–Sc*	*M–Sp*	*Sp–Sc*
Apple fruit (w.)	29	28	3·5
Bean leaf (unw.)	18	9	14
,, (inj.)	18	8	9
Eucharis Mastersi (w.)	17	12	10
Begonia Haageana (w.)	19	15	5
B. heraclaefolia (w.)	31	12	9
B. semperflorens (w.)	21	13	9
B. argenteo-guttata (w.)	22	20	6
Lilac (unw.)	40	21	21
,, (w.)	36	23	8
Lily of the Valley (w.)	22	15	9

In all these inoculation experiments it was interesting to note that each strain produced in a general way its particular growth characteristics on the diseased portions of the tissues. The mycelial strain *M* showed long strands of mycelium radiating out from the point of inoculation; strain *Sp* produced abundant spores over the diseased area; while strain *Sc* produced a very thin mycelial weft. In the case of the last strain sclerotia were not observed, probably because the individual experiments were not continued for a sufficiently long time to allow of sclerotial development. Berkeley (1) similarly notes that the various strains tested by him tend to show on the host the same general features as characterise them in culture.

Examination of certain physiological features of strains in relation to parasitic vigour.

Considerable attention has been devoted by numerous investigators to the fungus *Botrytis cinerea* in the attempt to analyse physiologically the phenomenon of parasitism. Since the pioneer work of de Bary (7) it has been known that fungi of the type of *Botrytis* are able to kill the host tissue in advance of their growth. The physico-chemical nature of the active principle responsible for this "action in advance" has been examined in detail by Brown (2). In addition to this chemical activity, fungi also appear to possess the power of mechanically penetrating plant membranes, a feature first clearly emphasised by Miyoshi (10). It was natural therefore to attempt to correlate the varying degree of parasitic vigour as illustrated by the three strains of *Botrytis* used in this work with their respective capacities for producing the active cell-attacking substance ("pectinase") or with their capacities for mechanically penetrating

membranes. In carrying out either of these comparisons the chief difficulties met with are of a purely technical nature.

The attempt to correlate parasitic activity with enzymic content of the fungus was made by Harter and Weimer (9) for various species of *Rhizopus* (*R. Tritici, R. nigricans, R. microsporus, R. chinensis,* etc.). Their method consisted in growing the various species in a somewhat large quantity of nutrient in conical flasks and testing both the cultural fluid and an extract of the mycelium for presence of the pectinase enzyme. The enzymic activity of the various solutions tested did not appear to be correlated in any way with the parasitic vigour of the strains from which these solutions were derived. They also found that there was no correlation between the amounts of intra- and extra-cellular enzyme present in the various cultures.

The problem of obtaining a quantitative estimate of the amount of enzyme formed by the fungus is complicated by the fact that, as was shown by Brown (3), the activity of the extract obtained from one particular strain varies very greatly with the manner of preparing it. For example, in any given culture of the fungus, the amount of enzyme extractable from the hyphae (or present in the culture liquid) goes through a grand-period curve, *i.e.* rises to a maximum in a few days and then falls off rapidly. A satisfactory comparison would thus entail very considerable experimental labour. Nevertheless, since the three strains dealt with in this work showed such distinct differences in parasitic vigour, it was considered that a comparison of the pectinase content of the three strains might be of interest. According to Brown, the maximum concentration of enzyme, both in the hyphae and in the nutrient, is reached at about the second day from sowing when a dense suspension of spores is germinated in a shallow layer of nutrient medium. It was decided therefore to follow Brown's technique and to make the various extractions at about the time when the maximal concentration of enzyme was present.

(1) *Comparison of Pectinase Content.* Spore suspensions of the three strains were prepared free from mycelium by filtration through fine muslin. The spores were centrifuged down in graduated tubes and the volume of spores determined. By this means it was possible to prepare spore suspensions of the three strains with approximately the same concentration of spores in each. These suspensions (in turnip extract) were then sown on flat glass plates in moist Petri dishes and allowed to germinate and grow for two to two and a half days at laboratory temperature. The weft of germinated spores was then taken off, washed, dried and ground up with silver sand. It was then extracted with water in a standard manner. The various extracts

were tested on potato discs of standard thickness and the time required for complete maceration determined. The pectinase content of the liquid in which the spores had germinated was similarly estimated.

On account of the large amount of apparatus required for the preparation of even a small quantity of ground germinated spores, it was not possible to prepare the material simultaneously for the three strains. The method adopted was therefore to accumulate material of one strain and keep it in the form of dry powder until a stock of material of the other two strains was likewise accumulated. The extracts were then made simultaneously and tested on discs of the same potato. The experiment was repeated four times, with the results given in Table V.

Table V. *Giving the times taken for maceration of potato discs by the enzymic extracts of the strains Sc, M and Sp.*

Strain	Exp. 1	Exp. 2	Exp. 3	Exp. 4
Sc	30 mins.	40 mins.	45 mins.	1 hr. 10 mins.
M	1 hr. 20 mins.	1 hr. 10 mins.	1 hr. 10 mins.	1 hr.
Sp	1 hr. 15 mins.	1 hr. 20 mins.	1 hr. 15 mins.	1 hr. 5 mins.

In order to avoid the error due to changing laboratory temperature during the successive germination periods, a further series was carried through in which the material was prepared from sowings of two strains made simultaneously and growing side by side. The results of this comparison in pairs are given in Table VI.

Table VI. *A comparison of the times taken for the maceration of potato discs by the enzyme pectinase prepared from two strains at a time.*

Strain	Time required for maceration
Sc	45 mins.
M	50 mins.
Sc	45 mins.
Sp	1 hr. 30 mins.
M	1 hr.
Sp	1 hr. 20 mins.
Sc	1 hr. 10 mins.
Sp	1 hr. 20 mins.
M	35 mins.
Sp	1 hr. 40 mins.

The figures given in Tables V and VI show a considerable amount of irregularity. Thus, in Table V, strain *Sc* furnished a stronger enzymic extract than the other two (Exps. 1–3); in Exp. 4 the enzymic extracts were of equal strength in the three cases. A similar lack of consistency is shown in the results given in Table VI. The figures, however, give no indication that the enzymic activity of the extracts obtainable from the weakly

parasitic strain *Sc* is less than that of corresponding extracts from the active strain *M*. In fact, the general weight of the evidence points in the opposite direction. The most active extracts that were obtained were from strain *Sc*.

These results confirm the findings of Harter and Weimer already cited. One cannot, however, doubt that the pectinase enzyme plays an important part in the progress of parasitic attack. If the excretion of enzyme by the attacking fungus is the factor which limits the rate of parasitic advance, it seems probable that the technique of extraction will have to be modified if data applicable to the problem are to be obtained. There is no evidence that the weakly parasitic strain produces less enzyme than the active one when the strains are grown on turnip extract and when the enzymic preparations are tested on potato discs. The question therefore arises whether a different result would be obtained if the fungi were grown in juice of the particular host plant concerned and the enzyme tested on tissue of that plant. Work along this line is projected. An alternative assumption is that all three strains used in these experiments are capable of secreting the enzyme in sufficient quantity for their needs, so that the concentration of enzyme present does not act as a limiting factor in controlling attack.

(2) *Comparison of the Penetrative Capacity*. The mechanical penetrating power of the three strains was tested by growing them on a series of formalised gelatine membranes of graded hardness, prepared after the manner described by Brown (4). Strips were cut from a gelatine sheet obtained by pouring a 5 per cent. gelatine solution over a mercury surface and allowing to dry in a current of air. The strips, cut to a suitable length, were then immersed in a series of alcohol-water mixtures for twenty-four hours. After this they were transferred to a series of the same strengths of alcohol containing 10 per cent. formalin. After fixing for twenty-four hours they were thoroughly washed several times in sterile water to remove all traces of formalin and then allowed to soak overnight in dilute sterile turnip extract. The strips were then dried on the surface and placed on glass slides in moistened Petri dishes. On each strip were placed a few drops of a spore suspension of one strain, the nutrient being of the same strength as was used for soaking the membranes. The suspension was made very dilute so that there were relatively few spores in each drop. The dishes were kept at the ordinary laboratory temperature. After two days, the strips were examined by inverting the slides and focusing with the lower power of the microscope. The hyphae that had penetrated appeared at a higher focus than those which remained on the surface. Penetrating hyphae were furthermore

easily recognisable by their characteristic corkscrew-like manner of growth.

The results are shown in Table VII. The percentage figures given in the table refer to the alcohol-water mixtures in which the membranes were graded (0 per cent. = water). The higher the alcohol content in the mixture used for grading, the harder the resultant membrane.

Table VII. *Showing penetration of formalised gelatine membranes by the three strains.*

Strain	0 %	10 %	20 %	30 %	35 %	40 %	45 %	50 %	60 %	70 %
Sc	+++	++	++	+	+	(+)	(+)	–	–	–
M	++++	+++	+++	++	++	(+)	(+)	–	–	–
Sp	+++	++	++	+	+	(+)	(+)	–	–	–

++++ = abundant hyphae penetrating.
+++ = less ,, ,,
++ = moderate ,, ,,
+ = few ,, ,,
(+) = hyphae penetrating only a short distance into the membrane.
– = no penetration.

The results of Table VII show that all three strains appear to have much the same power of mechanical penetration, so that the differences in parasitic power cannot be explained on the basis of different penetrating powers.

In the earlier part of this paper, where the cultural features of these strains were under consideration, it was pointed out that the strain *Sc* had the slowest rate of growth. This strain is also the least active parasitically. Whether these two features are connected or not is a question which will require further study. Again, it was noted that the strain *M* showed a marked tendency to the formation of attachment organs when in contact with a solid substratum. It might thus be suggested that the greater virulence of strain *M* is associated with its greater capacity for the formation of attachment organs, but it is not clear in what way this would function other than in a greater secretion of enzyme or a greater power of mechanical penetration. In neither of these respects is there as yet any evidence that strain *M* is in any way superior to either of the two weaker strains.

The author wishes to take this opportunity of expressing his thanks to Professor W. Brown at whose suggestion this investigation was begun and under whose general supervision it was carried out.

Summary.

1. The growth features of three strains of *Botrytis cinerea* were examined on a variety of media. One strain (*Sc*) proved to have a strongly marked sclerotium-forming tendency, strain *M* showed a general tendency towards the development of

aerial mycelium, and strain *Sp* was characterised by its freely sporing habit.

2. The intensity with which the various characters were manifested varied somewhat from medium to medium, but the general tendencies as noted above were observable throughout.

3. The effect of high atmospheric humidity was to increase the tendency to sclerotium formation and to diminish the tendency to sporulation. A similar effect produced by absence of light was indicated.

4. A definite difference in spore size and shape was shown as between strain *Sp* on the one hand and strains *Sc* and *M* on the other.

5. On the majority of media tested, strain *Sc* differed from the other two in showing a much slower rate of growth.

6. Inoculation experiments with a number of host plants showed that strain *M* was the most actively parasitic. No evidence of selective parasitism was obtained.

7. An analysis of the factors responsible for the differences in virulence observed was attempted. As far as the data could be interpreted, it was shown that the varying degree of virulence could not be ascribed to varying capacities of the strains for secreting the pectinase enzyme. It also appeared that the differences in parasitic power shown by the three strains could not be explained on the basis of different powers of mechanical penetration. A test of the three strains in the latter respect showed that they all possessed approximately the same penetrative power as judged by their behaviour on a series of formalised gelatine membranes of graded hardness.

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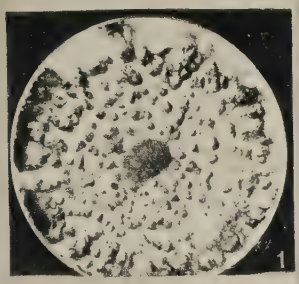
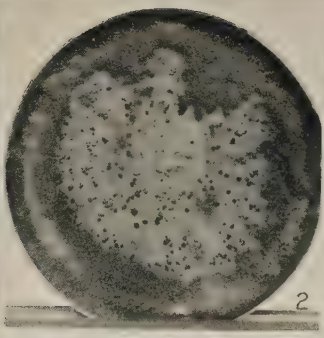
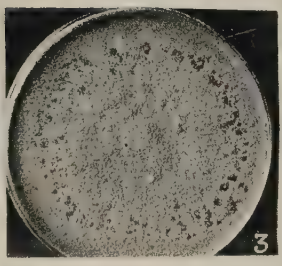
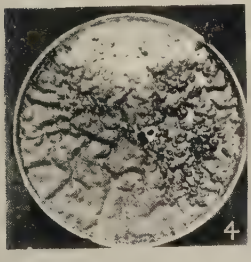
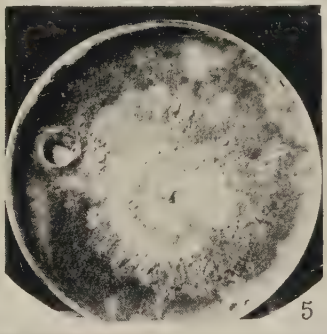
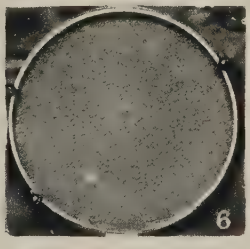


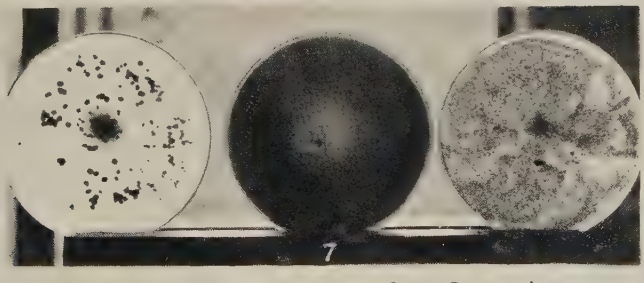












Sc M Sp Controls

BOTRYTIS CINEREA PERS.

EXPLANATION OF PLATE II.

Fig. 1. Strain *Sc* on potato-mush agar.
Fig. 2. Strain *M* on potato-mush agar.
Fig. 3. Strain *Sp* on potato-mush agar.
Fig. 4. Strain *Sc* on glucose-starch-peptone synthetic medium.
Fig. 5. Strain *M* on glucose-starch-peptone synthetic medium.
Fig. 6. Strain *Sp* on glucose-starch-peptone synthetic medium.
Fig. 7. Strains *Sc*, *M* and *Sp* respectively on glucose-starch-asparagin agar.
Fig. 8. Rates of attack by strains *Sc*, *M* and *Sp* on wounded leaves of lilac.

THE GONIDIUM COMMON TO MANY LICHENS.

By Robert Paulson, F.L.S., F.R.M.S.

(With Plate III.)

A MORE or less animated discussion respecting the exact nature of lichen gonidia has been in progress since Schwendener, 1867, published the epoch-making paper which made known his opinion that the gonidium of a lichen thallus is in reality an alga, and that the bright green spherical gonidium is identical with *Cystococcus humicola* Naeg.

One result of the great interest aroused by the advancement of this hypothesis was that investigators, Rees and Woronine, 1871, and Bornet, 1872, began experiments in building up the lichen thallus by means of culture methods.

This met with considerable success; it proved possible to obtain a lichen thallus by placing together the germinating spores of a lichen and the isolated gonidia from the thallus.

Stahl, 1877, succeeded so far as to be able to observe the gradual development of a complete lichen thallus even to the formation of perithecia and spores.

As time elapsed a perplexing confusion developed concerning the precise identity of the spherical green alga common to a number of lichens. Authors expressed diverse opinions the result of which was that synonyms and new combinations such as *Chlorococcum humicola* (Naeg.) Rabenh. (= *Cystococcus humicola* Naeg. pro parte, *Chlorococcum viride* Ag. including *Chlorosphaera limicola* Beyerinck), found a place in lichen literature.

Treboux, 1912, on publishing the result of his investigation respecting the gonidium of *Xanthoria parietina*, stated that this alga can be distinguished by its central, massive, star-shaped chromatophore which includes a central pyrenoid. Under cultivation it produces zoospores. For this alga he retained the name

Cystococcus humicola Naeg. although he had considerably extended Naegeli's diagnosis.

Chodat, 1913, wrote that Treboux had clearly appreciated the differences that separate *Chlorococcum Menegini* = *Chlorella infusionum* Beyerinck from the alga of many lichens, but added that at no time did Naegeli attribute to his alga a star-shaped or lobed chromatophore nor did he mention zoospores.

Puymaly, 1924, compiled a brief account of the confused state of nomenclature that then existed, and concluded that it was advisable to recognise, in the gonidium of *Xanthoria parietina*, and many other lichens, a new genus of alga, which he named *Trebouxia*. The necessity for such a change he supported by the statement that

(*a*) *Cystococcus* Naeg. is *Chlorococcum* Fries.

(*b*) The gonidium of *Xanthoria parietina* is *Trebouxia* Puym.

(*c*) *Cystococcus* Hedlum belongs to the genus *Prasiola*.

(*d*) *Cystococcus humicola* Gerneck is in all probability a *Dictylococcus*.

There is at present a lack of agreement respecting the exact form of the chromatophore of the alga of *Xanthoria parietina*. The reason for the difference of opinion is presumably due to the changes in appearance of the microscope image as seen under slight difference of focus or under various conditions of illumination. It may also be due partly to the absence of illustration, of any kind, relating to the published descriptions by recent writers.

As it is mainly due to the alleged form of the chromatophore that the need for the new genus, *Trebouxia*, arose, there is a clear necessity for the nearest possible approximation to the form, by delineation or photography, to accompany the published descriptions respecting it.

A block, described as after Chodat, has been used to illustrate the form of the chromatophore of *Trebouxia*. On this block the "equatorial" circle of the spherical body has a cogwheel-like appearance with indentations equal to a depth of one-seventh of the diameter of the circle; but this illustration does not correctly represent the normal chromatophore of *Xanthoria parietina* when viewed microscopically under critical illumination.

A star-shaped or lobed form of chromatophore is not represented in the figures given by earlier writers, *e.g.* Woronine 1872, Bornet 1873, de Bary and Bonnier 1889. A lighter portion in the colour of the wall is sometimes slightly indicated. It is not evident on Pl. I, figs. 1–6, of a paper "On a Malay Form of *Chlorococcum humicola*" (5).

Accompanying Danilov's (6) account, 1910, of the relation

between gonidia and hyphae of lichens, there are eighteen photomicrographs of gonidia from *Evernia prunastri* and *E. furfuracea* shown in Pl. II. These photomicrographs are not sufficiently sharp to bring out all the details of the chromatophore but six of them (10, 11, 13, 14, 17 and 18) exhibit an arc, sometimes equal to a semicircle, of the equatorial line of this body. These arcs are all smooth on the outer side.

When describing the gonidia of *Cladonia digitata* and *Evernia prunastri* (7, 8), 1920, I included photomicrographs of the gonidia of *Cladonia*, with a magnification of up to 2500, and of *Evernia* up to 1800 diameters. A vast majority of the chromatophores exhibit *a perfectly smooth outer surface* at the equator, the only position where the true form of the chromatophore can be distinguished.

When examining the gonidium, as it exists in the lichen thallus, it is of advantage to know something of the climatic conditions at the time the material was collected, for at certain periods, such as the return to mild weather after a severe winter, or on the occasion of heavy rain following a long period of drought, the gonidia will probably be in active sporulation and during this unstable condition, they may show, occasionally, a somewhat irregular form.

The methods of examination employed were varied, but the freshly gathered specimens were always thoroughly washed in rapidly running tap water to remove stray algae that might be present upon the surface. Minute portions were then cut from the edge and from the median part of the thallus and teased out under water on a micro-slide. To some of the preparations dilute glycerine-alcohol was added and to a small number of these a weak solution of safranine in addition, for photographic purposes. Some of the material, immediately after the washing process, was fixed in Schaffner's chrom-acetic solution before being dissected on the slide.

On a previous occasion when *Cladonia* and *Evernia* only were used, small portions of the thallus were taken through the paraffin process and afterwards stained with Haidenhain's iron-haematoxylin.

The result has been always the same as regards the chromatophore of the alga of *Xanthoria, Parmelia, Evernia, Physcia, Cladonia* and other lichens, *i.e.* the *outer surface was found to be smooth*; on no occasion, except when sporulation was in evidence, did any irregularity appear and then it was only slight. No deep indentation or conspicuous lobing, even under a magnification of three thousand five hundred diameters (Pl. III, fig. 3) was observed.

The chromatophore of *Xanthoria* is approximately a spherical

translucent body, crowded with minute green corpuscles (chloroplasts) and surrounded by a colourless band that is limited on the outer side by a smooth cell wall. It is an object that requires precise manipulation of the microscope, and the highest magnification, in order that the image formed may be a reliable one.

Gerneck noted this granular structure in the chromatophore of an alga which he decided was *Cystococcus* but which afterwards became known as *Dictylococcus* Wille. When writing of it he said: "*Cystococcus* will be characterised, not by a bell-shaped chromatophore, that is one with an opening on the side, it will possess on the contrary a large number of chlorophyll corpuscles, on the periphery, of the form usual to the higher plants." The name of the alga has been changed, but Gerneck's diagnosis describes adequately the granular condition of the chromatophore of the alga common to many lichens. The corpuscles under certain conditions appear as so many projections. The touchstone whether this is correct is the equatorial circle of the chromatophore which, in the photomicrographs of Pl. III, figs. 1, 2, 3 and 5, exhibits a perfectly smooth line on the outer side, when in true focus, but which appears as a fuzzy or shaggy outline, that might be described as star-shaped or lobed, the more the alga is removed from the true, central focus (Pl. III, fig.3).

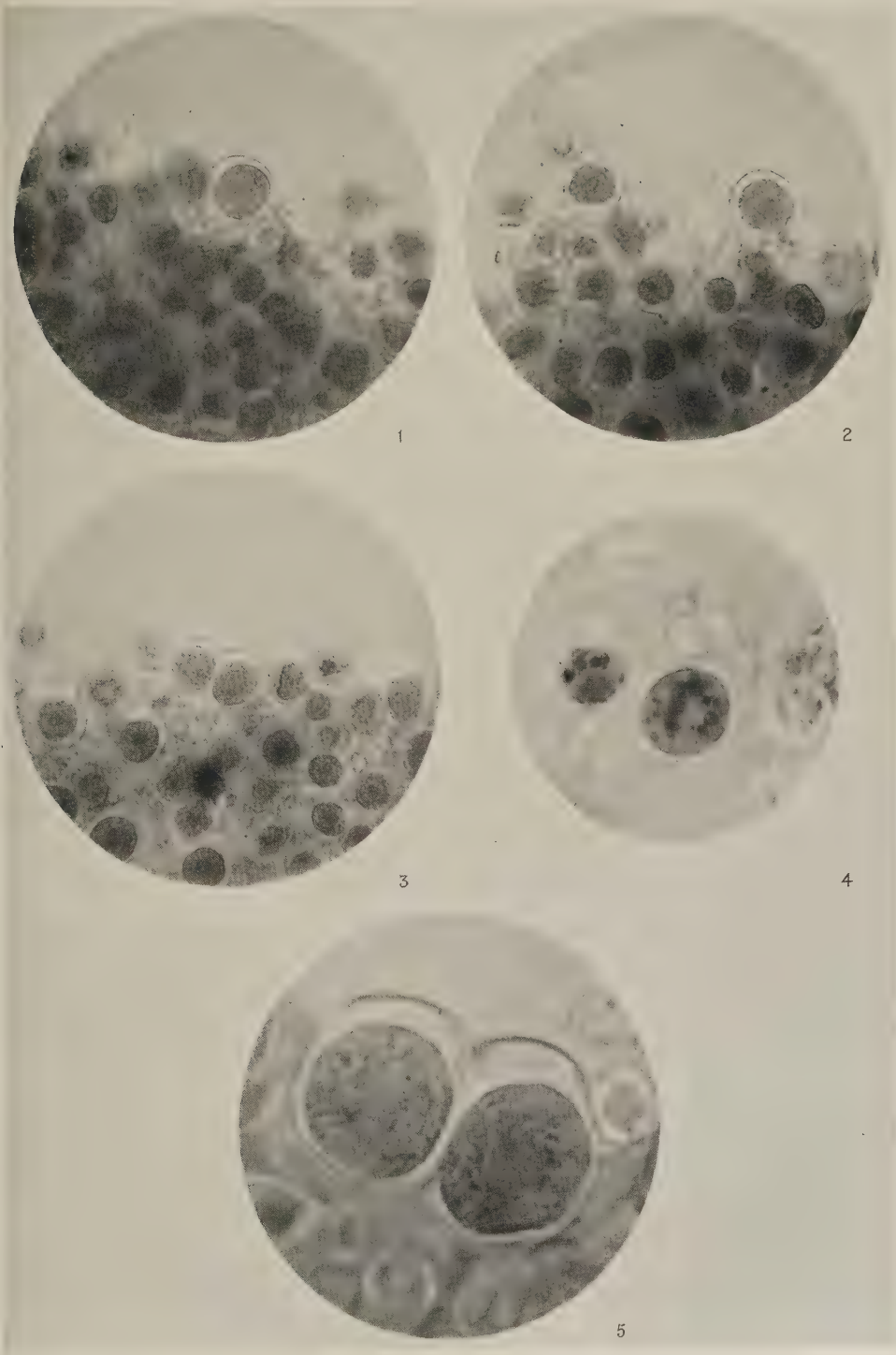
Trebouxia Puymaly does not present correctly the common gonidium of lichens as in *Xanthoria parietina*. It has no relation to the observed form as seen in the photomicrographs (Pl. III, figs. 1 and 2) which depict the chromatophore as without irregularity on the outer surface.

The reliability of photomicrography, when produced by a recognised expert, is unquestioned.

The results obtained, as seen on Pl. III, make it clear that the genus *Trebouxia* required revision.

It is possible, owing to the smooth exterior of the chromatophore of *Cladonia digitata* that the late Professor G. S. West, judging from preparations forwarded at his request, replied, shortly after receiving them (May, 1918) that *Protococcus viridis* certainly occurs in some lichens, but species of *Chlorella* are perhaps more frequent"; and six months later (November, 1918), "I will keep one of the slides, if I may, and return the others....The gonidia are nearer some of the forms of *Chlorella* than anything else I am acquainted with."

I take the opportunity of recording my grateful thanks to Mr J. H. Pledge for having again given the services of his highly technical skill in photomicrography in the production of the illustrations to this paper, without which it would not have



LICHEN GONIDIA

been possible to convey clearly and authoritatively a true representation of the lichen gonidia.

NOTE. A paper by Werner (9) just to hand has among the illustrations a few drawings of the gonidia of *Xanthoria parietina*. Among them, two that are mature, and several daughter cells, have a chromatophore perfectly smooth on the surface. Werner says however, "Chaque algue est munie d'un chromatophore étoilé, parfois *rond*." This variation mentioned is evidently the result of change of focus.

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EXPLANATION OF PLATE III.

Figs. 1 and 2. Portions of the thallus of *Xanthoria parietina* each of which shows a gonidium focused on the equatorial line. The sharp outline of the chromatophore has for the most part an unbroken curve. × 1000.

Fig. 3. Gonidia as above. Here on the extreme left they are evidently out of focus, the outline of the chromatophore is not well defined but is occasionally fringed in appearance as in the uppermost gonidia on the left. × 1000.

Fig. 4. Isolated gonidia of *Evernia prunastri* undergoing changes previous to sporulation. In the larger the spherical surface of the chromatophore is still unbroken; in the smaller there are signs of the surface breaking up. × 1800.

Fig. 5. Two gonidia of *X. parietina* highly magnified; the surface of the upper hemisphere of the chromatophore appears to be rough but the equatorial circle decides it is otherwise, as it is not in the least irregular. The rough appearance is optical and not real. × 3000.

LIST OF COMMON NAMES OF BRITISH PLANT DISEASES.

(Compiled by the Plant Pathology Sub-Committee of the British Mycological Society)

Introduction

In view of the ever increasing importance of a knowledge of the various diseases that affect cultivated plants it is desirable that there should be uniformity in the popular nomenclature of such diseases in the British Isles. The present list of Common Names of the more important diseases of those crop and ornamental plants which are grown on a considerable scale in the British Isles, has been drawn up by the Plant Pathology Sub-Committee of the British Mycological Society, with the object of selecting for each disease a *single* common name wherever possible, the use of which it is desired to encourage throughout the British Isles and the Empire. By this means it is hoped to avoid the confusion often caused by the use of more than one common name for the same disease. Growers of agricultural and horticultural crops are being brought more and more into intimate contact with plant pathologists, and it is thought that co-operation between them will be facilitated, and misunderstandings avoided, by the adoption of these standard names. The list is based primarily on the "Report on the occurrence of Fungus, Bacterial and Allied Diseases of Crops in England and Wales for the years 1922–24," issued as No. 52 of the *Miscellaneous Publications of the Ministry of Agriculture and Fisheries* in 1926.

With parasitic diseases the scientific names of the causative parasites have been included, since only too frequently in the past there has been confusion between the name of the disease and the name of the parasite. The list is therefore arranged in two parallel columns; on the left, under the name of the host plant, will be found the common name recommended for the disease; on the right, the scientific name of the parasite.

Care has been taken to ensure that the correct scientific name and authority* are given for each parasite, according to the International Rules of Botanical Nomenclature. Where investigation has shown that a scientific name hitherto in common use

* The method adopted for quoting authorities has been to place the name of the original author of the specific name in parenthesis where there has been a transference to another genus. This parenthetical name, though frequently omitted by workers, is useful in showing that there has been such a transference; otherwise it might be assumed, in the absence of synonyms, that the fungus was a newly described one. For explanation of the abbreviations of the names of authorities, see page 174.

is incorrect, it has been amended. It is hoped therefore that the names in this list will be used by plant pathologists when referring to the various parasites concerned.

Many of the diseases are prevalent in foreign countries as well as in the British Isles, and the common names applied to them in certain of these countries have been inserted in the following order: (1) United States of America, (2) France, (3) Italy, (4) Germany, (5) Holland, (6) Denmark. In the list these numerals indicate the respective countries. The names of diseases occurring in the United States are inserted only when they differ from those recommended. These foreign names are not necessarily used by the grower, but are often found in the scientific and popular plant pathological literature of the countries concerned. The foreign names for Downy Mildew, Mildew and Rust are given on p. 142, and are not repeated under each host.

For convenience the host plants are arranged in groups, such as Cereals, Vegetables, etc., and the causative agents of the diseases are given under each host in the following order: Viruses*, Bacteria, Myxomycetes, Phycomycetes, Ascomycetes, Basidiomycetes, Fungi Imperfecti, Non-parasitic.

Nearly all the common names given in this list are already in general use. If a disease happens to be known by more than one name in different parts of the country, *e.g.* Finger-and-Toe, Club Root, Anbury, one of these names has been selected. Some of these alternative names have been inserted, however, beneath the chosen name, because, without them, obscurity might exist in the minds of a few growers or others. A few other alternative common names are included because they appear to be the chief or only ones used locally or in certain parts of the Empire. Thus, in New Zealand, apple Scab is apparently invariably called Black Spot. Other more or less common names have been omitted deliberately, and it is hoped that in time not only will they have been forgotten, but that the alternative common names now included will also have fallen into disuse. In some instances, where one parasite causes two or more distinct types of disease symptoms, particularly in different parts of the host, a name for each is recommended, *e.g.* Blossom Wilt, Spur Blight, Wither Tip and Brown Rot in plums. Occasionally, where the existing common name is inappropriate for technical reasons, a new name has been coined; thus the disease caused by *Cystopus candidus* has been designated White Blister instead of White Rust since the parasite is not related to the true Rusts. If until now there has been no common name for a disease, one has been suggested, as *e.g.* Black

* The term "virus" as used in the present list does not necessarily mean "filtrable virus."

Pustule for the disease of currant bushes caused by *Plowrightia ribesia*.

Under the scientific names of the parasites synonyms are often given, especially those which still occur frequently in the literature, since to omit them might lead to obscurity. For the same reason the names of the conidial or other imperfect stages of the parasites are inserted when these are still frequently used. If, however, the perfect stage of a particular parasite has not yet been recorded in the British Isles, a note to that effect is inserted. For example in Black Spot of roses, caused by *Diplocarpon Rosae* Wolf, only the conidial stage, *Actinonema Rosae* (Lib.) Fr., is yet known in this country. Certain other explanatory notes are also included.

Reference is made in the list to the Damping-off diseases under only a few of the chief hosts, because these diseases affect many kinds of plants, especially when raised in seed-beds, and because several different parasites cause them. These Damping-off diseases are known in foreign countries as: (2) fonte des semis, (3) marciume delle piantine nei semenzai, (4) Umfallen der Keimpflanzen, (5) kiemschimmels, smucht, (6) rodbrand. The chief causes of "Damping-off" in the British Isles are *Pythium de Baryanum*, *Phytophthora parasitica* and *P. cryptogea*, *Corticium* (*Rhizoctonia*) *Solani*, *Botrytis cinerea* and *Fusarium* spp. The seedling disease caused by *Botrytis cinerea* is distinguished in France as "maladie de la toile," and in Italy as "mal della tela."

The foreign names for Downy Mildew are (2) mildiou, Peronospora, (3) Peronospora, muffo, (4) falscher Mehltau, (5) valsche meeldauw; and for ordinary Mildew (1) powdery mildew, (2) oidium, blanc, (3) nebbia, oidio, (4) Mehltau, (5) meeldauw, wit, (6) meldug. The Rusts are (2) rouille, (3) ruggine, (4) Rost, (5) roest, (6) rust. The foreign names therefore are not given except in special cases.

To all those British and foreign mycologists who have kindly assisted in compiling this list the Sub-Committee wish to tender their hearty thanks. It is realised that perfection has not been attained in the list now presented, which is to be regarded as to some extent provisional and tentative, and suggestions for the improvement of the list will be welcomed. The Sub-Committee express the hope that similar lists will be drawn up in other parts of the Empire, where this has not already been done, so that in time there will be available a complete record of the diseases of crop plants that occur within the Empire.

CEREALS

WHEAT (*Triticum*).

Mildew ... ... *Erysiphe graminis* DC.

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.

(2) ergot, miellat for *Sphacelia* stage, (3) chiodo melata, (4) Mutterkorn, (5) moederkoren, (6) meldrøjer.

The conidial stage (Honey Dew) was formerly known as *Sphacelia segetum* Lév.

Whiteheads ... ... *Ophiobolus graminis* Sacc.
(Take All.)

(1) foot-rot, (2) piétin, (3) mal del piede, (4) Fusskrankheit, (5) halmvoetziekte, halmdooder, (6) draeber, fodsyge.

Bunt ... ... *Tilletia Caries* (DC.) Tul.
(Stinking Smut.) (= *T. Tritici* (? Bjerk.) Wint.)

(2) carie, (3) carie, golpe, carbone fetido, (4) Steinbrand, (5) steenbrand, stinkbrand, (6) stinkbrand.

T. foetens (Berk. & Curt.) Trel. (= *T. laevis* Kühn) appears to be very rare in Britain.

Loose Smut ... ... *Ustilago Tritici* (Pers.) Jens.

(2) charbon, (3) carbone volante, (4) Flugbrand, (5) stuifbrand, (6) støvbrand.

Black Rust ... ... *Puccinia graminis* Pers.

(1) stem rust, (2) rouille noire, (4) Schwarzrost, (5) zwarte roest, (6) sortrust.

Yellow Rust ... ... *Puccinia glumarum* (Schm.) Erikss. & Henn.

(1) stripe rust, (2) rouille jaune, (3) ruggine gialla, (4) Gelbrost, (5) gele roest, (6) gulrust.

Brown Rust ... ... *Puccinia triticina* Erikss.

(1) orange leaf rust, (2) rouille brune, (3) ruggine bruna, (4) Braunrost, (5) bruine roest, (6) brunrust.

Twist ... ... *Dilophospora Alopecuri* (Fr.) Fr. (= *D. graminis* Desm.)

(4) Federbuschsporenkrankheit.

Leaf Spot ... ... *Septoria Tritici* Desm.

(1) speckled leaf blotch, (2) nuile, (3) seccume, (4) Schwarzfleckigkeit, (6) hvedensgraapletsyge.

Glume Blotch ... ... *Septoria nodorum* Berk. (= *S. glumarum* Pass.)

Black Mould ... ... *Cladosporium herbarum* (Link) Fr. and *Alternaria* spp.

(2) noir, (3) nero, (4) Schwärze, (5) zwart der granen, (6) sort skimmel.

Parasitism doubtful.

Foot Rot and Ear Blight *Fusarium avenaceum* (Fr.) Sacc. and *F. culmorum* (W. G. Sm.) Sacc.

(2) piétin, (3) mal del piede, (4) Fusskrankheit, (5) kiemschimmel, (6) slimskimmel.

OATS (*Avena*).

Halo Blight ... ... *Bacterium coronafaciens* Ch. Elliott

(4) Weissfleckenkrankheit.

The organism has not yet been isolated from British material.

Mildew ... ... *Erysiphe graminis* DC.

Whiteheads ... ... *Ophiobolus graminis* Sacc.

For foreign names see under Wheat.

Covered Smut ... ... *Ustilago Kolleri* Wille (= *U. laevis* (Kellerm. & Swing.) Magn.)

(2) charbon, (3) carbone, (4) gedeckter Haferbrand, (5) bedekte haverbrand, (6) daekket havrebrand.

Loose Smut ... ... *Ustilago Avenae* (Pers.) Jens.

(2) charbon, (3) carbone volante, (4) Flugbrand, (5) haverstuifbrand, (6) nøgen havrebrand.

Black Rust ... ... *Puccinia graminis* Pers.

For foreign names see under Wheat.

Crown Rust ... ... *Puccinia Lolii* Niels. (= *P. coronifera* Kleb.)

(2) rouille couronnée, (3) ruggine coronata, (4) Kronenrost, (5) kroonroest, (6) kronrust.

Leaf Spot ... ... *Helminthosporium Avenae* (Bri. & Cav.) Eid.

(1) leaf blight, (2) taches des feuilles, (6) mørkpletsyge.

Grey Leaf ... ... Non-parasitic.

(4) Dörrfleckenkrankheit, (5) veenkoloniale ziekte, (6) lyspletsyge.

BARLEY (*Hordeum*).

Mildew ... ... *Erysiphe graminis* DC.

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.

For foreign names see under Wheat.

Whiteheads ... ... *Ophiobolus graminis* Sacc.

For foreign names see under Wheat.

Net Blotch ... ... *Pyrenophora teres* (Died.) Drechsl. (*Helminthosporium teres* Sacc.)

(5) vlekkenziekte, (6) byggets bladpletsyge.

Loose Smut ... ... *Ustilago nuda* (Jens.) Rostr.

(2) charbon, (3) carbone volante, (4) Flugbrand, (5) naakte gerstebrand, (6) nøgen bygbrand.

Covered Smut ... ... *Ustilago Hordei* (Pers.) Kellerm. & Swing.

(2) charbon, (3) carbone, (4) gedeckter Gerstenbrand, (5) gerstesteenbrand, (6) daekket bygbrand.

Black Rust ... ... *Puccinia graminis* Pers.

For foreign names see under Wheat.

Yellow Rust ... ... *Puccinia glumarum* (Schm.) Erikss. & Henn.

For foreign names see under Wheat.

Brown Rust ... ... *Puccinia anomala* Rostr.
(Dwarf Rust.) ... (= *P. simplex* Erikss. & Henn.)

For foreign names see under Wheat.

Leaf Stripe ... ... *Helminthosporium gramineum* Rabenh.

(1) stripe disease, (3) striatura bruna, (4) Streifenkrankheit, (5) strepenziekte, (6) byggets stribesyge.

Leaf Blotch ... ... *Rhynchosporium Secalis* (Oud.) Davis (= *Marssonina Secalis* (Oud.) Magn.)

(1) scald.

RYE (*Secale*).

Mildew ... ... *Erysiphe graminis* DC.

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.

For foreign names see under Wheat.

Stripe Smut ... ... *Urocystis occulta* (Wallr.) Rabenh.
(1) stem smut, (2) carbon des tiges, (3) carbone del culmo, (4) Stengelbrand, (5) stengelbrand, (6) staengelbrand.

Black Rust ... ... *Puccinia graminis* Pers.
For foreign names see under Wheat.

Brown Rust ... ... *Puccinia secalina* Grove (= *P. dispersa* Erikss.)
For foreign names see under Wheat.

Leaf Blotch ... ... *Rhynchosporium Secalis* (Oud.) Davis (= *Marssonina Secalis* (Oud.) Magn.)
(1) scald.

PASTURE AND FORAGE CROPS.

RYE GRASSES (*Lolium*).

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.
For foreign names see under Wheat.

Crown Rust ... ... *Puccinia Lolii* Niels. (= *P. coronifera* Kleb.)
For foreign names see under Oats.

COCKSFOOT (*Dactylis*).

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.
For foreign names see under Wheat.

Choke ... ... *Epichloe typhina* (Fr.) Tul.
(2) quenouille, (3) mal della clava, (4) Erstickungsschimmel, (5) grastoperstikker, (6) skedesvamp.

Rust ... ... *Uromyces Dactylidis* Otth and *Puccinia glumarum* (Schm.) Erikss. & Henn.

TIMOTHY (*Phleum*).

Ergot ... ... *Claviceps purpurea* (Fr.) Tul.
For foreign names see under Wheat.

Rust ... ... *Puccinia Phlei-pratensis* Erikss. & Henn.

CLOVERS (*Trifolium*).

Downy Mildew ... ... *Peronospora Trifoliorum* de Bary

Mildew ... ... *Erysiphe Polygoni* DC.

Black Blotch ... ... *Dothidella Trifolii* (Pers.) Bayl. Elliott & Stansf. (*Polythrincium Trifolii* Kunze)

(1) sooty spot, (3) vaiolatura nera, (4) Schwarzwerden.

Rot ... ... *Sclerotinia Trifoliorum* Erikss.

(1) root rot, (2) chancre, (3) cancro, (4) Krebs, (5) kanker, (6) baegersvamp.

Leaf Spot ... ... *Pseudopeziza Trifolii* (Biv.-Bern.) Fuck.

(3) vaiolatura, (4) Blattfleckenkrankheit, (5) bladvlekkenziekte, (6) skivesvamp.

Mid-vein Spot ... ... *Mycosphaerella carinthiaca* Jaap

Rust ... ... *Uromyces Trifolii* (Hedw.f.) Lév.

This species occurs on *T. pratense*, *T. hybridum* and *T. incarnatum*. The two rusts on *T. repens* are *U. flectens* Lagerh. and *U. Trifolii-repentis* Liro.

Violet Root Rot ... *Helicobasidium purpureum* (Tul.) Pat. (*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

(2) rhizoctone violet, (3) mal vinato, (4) Wurzeltöter, (5) Rhizoctonia rot, (6) rodfiltsvamp.

Scorch ... ... *Kabatiella caulivora* (Kirchn.) Karak. (= *Gloeosporium caulivorum* Kirchn.)

(2) anthracnose, (3) antracnosi, (4) Stengelbrenner, (5) stengelbrand, (6) staengelsyge.

TREFOIL (*Medicago lupulina*).

Rot ... ... *Sclerotinia Trifoliorum* Erikss.

For foreign names see under Clovers.

Leaf Spot ... ... *Pseudopeziza Medicaginis* (Lib.) Sacc.

For foreign names see under Clovers.

Rust ... ... *Uromyces striatus* Schroet.

LUCERNE (*Medicago sativa*).

Crown Wart ... ... *Urophlyctis Alfalfae* (Lagerh.) Magn.

(2) tumeurs marbrées, (3) mal del gozzo, (5) knobbelvoet, (6) lucernebrok.

Downy Mildew ... ... *Peronospora Trifoliorum* de Bary

Rot ... ... *Sclerotinia Trifoliorum* Erikss.

For foreign names see under Clovers.

Leaf Spot ... ... *Pseudopeziza Medicaginis* (Lib.) Sacc.

For foreign names see under Clovers.

Violet Root Rot... ... *Helicobasidium purpureum* (Tul.) Pat.
(*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

For foreign names see under Clovers.

SAINFOIN (*Onobrychis*).

Chocolate Spot ... ... *Bacillus Lathyri* Manns & Taubenh.

Mildew ... ... *Erysiphe Polygoni* DC.

Rot ... ... *Sclerotinia Trifoliorum* Erikss.

For foreign names see under Clovers.

Rust ... ... *Uromyces Onobrychidis* (Desm.) Lév.

VETCHES (*Vicia*).

Chocolate Spot ... ... *Bacillus Lathyri* Manns & Taubenh.

Downy Mildew ... ... *Peronospora Viciae* (Berk.) de Bary

Rust ... ... *Uromyces Fabae* (Pers.) de Bary

PULSE.

BROAD AND FIELD BEAN (*Vicia*).

Chocolate Spot ... ... *Bacillus Lathyri* Manns & Taubenh.

Downy Mildew ... ... *Peronospora Viciae* (Berk.) de Bary

Rust ... ... *Uromyces Fabae* (Pers.) de Bary

Sclerotinia Disease ... *Sclerotinia Sclerotiorum* (Lib.) de Bary (= *S. Libertiana* (Lib.) Fuck.)

Leaf Spot ... ... *Ascochyta Fabae* Speg. and *Cercospora Fabae* Fautr.

DWARF AND RUNNER BEAN (*Phaseolus*).

Mosaic ... ... Virus.

Sclerotinia Disease ... *Sclerotinia Sclerotiorum* (Lib.) de Bary (= *S. Libertiana* (Lib.) Fuck.)

Blotch ... ... *Ascochyta Phaseolorum* Sacc.

Anthracnose ... ... *Colletotrichum Lindemuthianum* (Sacc. & Magn.) Bri. & Cav.

(2) anthracnose, (3) antracnosi, (4) Brennfleckenkrankheit, (5) vlekkenziekte.

PEA (*Pisum*).

Marsh Spot ... ... ? Bacterial.

(5) kwade harten, zwarte pitten.

Root Rot ... ... *Aphanomyces euteiches* Drechsl., and *Thielavia basicola* Zopf*

Downy Mildew ... ... *Peronospora Viciae* (Berk.) de Bary

Mildew ... ... *Erysiphe Polygoni* DC.

Spot ... ... *Ascochyta Pisi* Lib.

(1) blight, (2) taches noires, (4) Fleckenkrankheit, (5) vlekkenziekte, (6) aertesyge.

Recent investigations appear to show that *Mycosphaerella pinodes* (Berk. & Blox.) Niessl is not the perfect stage of this fungus, as was at one time thought.

POTATO (*Solanum tuberosum*).

Leaf Roll ... ... Virus.
(Leaf Curl.)

(2) enroulement, (4) Blattrollkrankheit, (5) bladrolziekte, (6) bladrullsyge.

Mosaic, Crinkle, etc. ... Virus.

* See note under Tobacco.

Streak ... ... Virus.

(4) Strichelkrankheit, (5) streepziekte.

Black Leg ... ... *Bacillus phytophthorus* Appel
(Black Stalk-Rot.) ... (= *B. atrosepticus* van Hall)

(2) jambe noire, (4) Schwarzbeinigkeit, (5) zwartbeenigheid, (6) sortbensyge.

Spraing ... ... ? Bacterial.
(Sprain, Internal Rust Spot.)

(1) internal brown spot, (2) taches en couronne, (4) Eisenfleckigkeit, (5) kringerigheid, (6) indwendig rustpletsyge.

"Spraing" is the Scottish word meaning a stripe, including the idea of variegation.

Common Scab ... ... *Actinomyces scabies* (Thaxt.)
(Brown Scab, Ordinary Scab.) Güss.
(= *Oospora scabies* Thaxt.)

(2) gale ordinaire, (3) rogna, (4) Schorf, (5) schurftziekte, (6) skurv.

Powdery Scab ... ... *Spongospora subterranea* (Wallr.)
(Corky Scab.) Lagerh.

(2) gale poudreuse, (3) crosta, (4) Pulverschorf, (5) poederschurft, (6) pulverskurv.

Wart Disease ... ... *Synchytrium endobioticum*
(Black Scab.) (Schilb.) Perc.
(= *Chrysophlyctis endobiotica* Schilb.)

(1) black-wart, (2) gale verruqueuse, (3) rogna nera, (4) Kartoffelkrebs, (5) wratziekte, (6) kartoffelbrok.

Blight ... ... *Phytophthora infestans* (Mont.) de Bary

(1) late blight, (2) mildiou, (3) marciume, (4) Kraut- u. Knollenfäule, (5) aardappelziekte, (6) kartoffelskimmel.

Pink Rot... ... ... *Phytophthora erythroseptica* Pethybr.

(5) roodrot.

Stalk Break ... ... *Sclerotinia Sclerotiorum* (Lib.) de Bary
(Stalk Disease, "Haughing.") (= *S. Libertiana* (Lib.) Fuck.)

Black Scurf and Stem Canker ... ... *Corticium Solani* Bourd. & Galz.
(= *Rhizoctonia Solani* Kühn)

(1) rhizoctoniose, (2) variole, (4) Pockenkrankheit, Fussvermorschung, (5) lakschurft, (6) graaben.

Violet Root Rot (Copper Web.) ... *Helicobasidium purpureum* (Tul.) Pat. (*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

(1) red root, (2) rhizoctone, (3) mal vinato, (4) violetter Wurzeltöter, (6) rodfiltsvamp.

Phoma Rot ... ... *Phoma tuberosa* Melh., Rosenb. & E. S. Schultz

Black Dot ... ... *Colletotrichum atramentarium* (Berk. & Br.) Taubenh. (= *C. tabificum* Pethybr., *Vermicularia varians* Ducom.)

(2) dartrose.

Grey Mould ... ... *Botrytis cinerea* Pers.

Dry Rot ... ... *Fusarium caeruleum* (Lib.) Sacc.

(2) pourriture sèche, (4) Trockenfäule, (5) Fusariumrot.

In the older English literature sometimes called "Winter Rot" and quite erroneously ascribed to the saprophyte *Nectria Solani* Reinke & Berth.

Verticillium Wilt ... *Verticillium albo-atrum* Reinke & Berth.

(2) verticilliose, (3) tracheo-verticilliosi, (4) Welkekrankheit, (5) Verticillium-ziekte, (6) kransskimmel-fodsyge.

Silver Scurf ... ... *Spondylocladium atrovirens* Harz (= *Phellomyces sclerotiophorus* Frank)

(1) dry scab, (2) gale argentée, (4) Silberflecken, (5) zilverschurft.

Skin Spot ... ... *Oospora pustulans* Owen & Wakef.

ROOT CROPS.

TURNIP AND SWEDE (*Brassica*).

Soft Rot (White Rot.) ... ... *Bacillus carotovorus* L. R. Jones, and *Pseudomonas destructans* Potter

Black Rot (Brown Rot.) ... ... *Pseudomonas campestris* Pamm.) E. F. Sm.

Finger-and-Toe ... ... *Plasmodiophora Brassicae* Woron (Club Root, Anbury.)

(1) club root, (2) hernie, (3) ernia, (4) Kropfkrankheit, (5) knolvoet, (6) kaalbrok.

White Blister ... ... *Cystopus candidus* (Pers.) de Bary (White Rust.)

(= *Albugo candida* (Pers.) O. Kuntze)

(1) White rust, (2) rouille blanche, (3) ruggine bianca, (4) Weissrost, (5) witterost, (6) hvidrust.

Downy Mildew ... ... *Peronospora parasitica* (Pers.) Tul.

Mildew ... ... *Erysiphe Polygoni* DC.

Dry Rot and Canker ... *Phoma Lingam* (Tode) Desm. (= *P. Napobrassicae* Rostr. and *Phoma oleracea* Sacc.)

(6) kaalroernes tørforraadnelse.

White Spot ... ... *Cercospora Bloxami* Berk. & Br.

Leaf Spot ... ... *Alternaria Brassicae* (Berk.) Bolle

MANGOLD AND BEET (*Beta*).

Mosaic ... ... Virus.

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.

(2) tumeur du collet, (4) Wurzelkropf, (6) krongalle.

Scab ... ... *Actinomyces scabies* (Thaxt.) Güss. and *A. tumuli* Millard & Beeley

Downy Mildew ... ... *Peronospora Schachtii* Fuck.

Rust ... ... *Uromyces Betae* (Pers.) Tul.

Violet Root Rot... ... *Helicobasidium purpureum* (Tul.) Pat. (Copper Web.)

(*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

For foreign names see under Potato.

Black Leg ... ... *Phoma Betae* (Oud.) Frank, *Pythium de Baryanum* Hesse, *Pythium aphanidermatum* (Eds.) Fitzp. and *Corticium Solani* Bourd. & Galz.

(2) pied noir, (4) Wurzelbrand, (5) wortelbrand, (6) rodbrand.

Heart Rot ... ... ? Non-parasitic or *Phoma Betae* (Oud.) Frank

(2) pourriture du coeur, (4) Herzfäule, (6) hjerteforraadnelse.

Leaf Spot ... ... *Cercospora beticola* Sacc.

Leaf Scorch ... ... *Sporidesmium putrefaciens* Fuck.

(4) Blattbräune. Parasitism doubtful.

VEGETABLES.

ASPARAGUS.

Rust ... ... *Puccinia Asparagi* DC.

Violet Root Rot ... *Helicobasidium purpureum* (Tul.) Pat. (*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

For foreign names see under Potato.

LEEK (*Allium Porrum*).

Soft Rot ... ... ? *Bacillus carotovorus* L. R. Jones

(3) batteriosi, marciume, (4) Bakterienfäule.

Smut ... ... *Urocystis Cepulae* Frost

(2) charbon, (3) carbone, (4) Zwiebelbrand, (5) uienbrand, zwartmop, (6) løgbrand.

Rust ... ... *Puccinia Porri* (Sow.) Wint.

White Rot ... ... *Sclerotium cepivorum* Berk.

(2) maladie blanche, (3) mal dello sclerozio, (4) Verschimmeln, (5) verschimmelen der uien.

ONION (*Allium Cepa*).

Soft Rot ... ... *Bacillus carotovorus* L. R. Jones

(3) marciume molle, (4) Bakterienfäule, (6) hvidbakteriose.

Downy Mildew ... ... *Peronospora Schleideni* Unger

Smut ... ... *Urocystis Cepulae* Frost

For foreign names see under Leek.

Rust ... ... *Puccinia Porri* (Sow.) Wint.

Smudge ... ... *Colletotrichum circinans* Vogl.
(2) anthracnose, (4) Brennfleckenkrankheit.

Black Mould ... ... *Aspergillus niger* van Tiegh.
(= *Sterigmatocystis nigra* van Tiegh.)
Parasitism doubtful.

White Rot ... ... *Sclerotium cepivorum* Berk.
For foreign names see under Leek.

Neck Rot ... ... *Botrytis Allii* Munn
(2) pourriture grise, (3) muffa grigia, (4) Grauschimmel, (5) grauwe schimmel, (6) drueskimmel.
B. byssoidea Walker and *B. squamosa* Walker are also sometimes associated with this disease in the United States.

SHALLOT (*Allium ascalonicum*).

Downy Mildew ... ... *Peronospora Schleideni* Unger

White Rot ... ... *Sclerotium cepivorum* Berk.
For foreign names see under Leek.

CABBAGE, CAULIFLOWER, etc. (*Brassica oleracea*).

Black Rot ... ... *Pseudomonas campestris* (Pamm.) E. F. Sm.
(3) batteriosi, marciume nero, (4) Braunfäule, Schwarzfäule, (5) bacterieziekte, (6) brunbakteriose.

Finger-and-Toe ... ... *Plasmodiophora Brassicae* Woron.
(Club Root, Anbury.)
For foreign names see under Turnip and Swede.

White Blister ... ... *Cystopus candidus* (Pers.) de Bary
(White Rust.)
(= *Albugo candida* (Pers.) O. Kuntze)
For foreign names see under Turnip and Swede.

Downy Mildew ... ... *Peronospora parasitica* (Pers.) Tul.

Ring Spot ... ... *Mycosphaerella brassicicola* (Fr.) Lindau
(4) Blattfleckenkrankheit, (5) bladvlekkenziekte, (6) kaalens bladpletsyge.

Stem Rot ... ... *Phoma Lingam* (Tode) Desm. (= *P. Napobrassicae* Rostr. and *P. oleracea* Sacc.)

(1) black leg, (3) cancro del fusto, (4) Krebsstrunke und Fallsucht, (5) vallers en kankerstronken.

Leaf Spot ... ... *Gloeosporium concentricum* (Grev.) Berk. & Br.

Grey Mould ... ... *Botrytis cinerea* Pers.

(2) pourriture grise, (3) muffa grigia, (4) Grauschimmel, (5) grauwe schimmel, (6) drueskimmel.

CRESS (*Lepidium*).

Damping-off ... ... *Pythium de Baryanum* Hesse

HORSE-RADISH (*Cochlearia*).

White Blister (White Rust.) ... ... *Cystopus candidus* (Pers.) de Bary (= *Albugo candida* (Pers.) O. Kuntze)

For foreign names see under Turnip and Swede.

Pale Spot ... ... *Ramularia Armoraciae* Fuck.

(1) leaf spot, (4) Blattfleckenkrankheit, (6) bladpletsyge.

RADISH (*Raphanus*).

Finger-and-Toe (Club Root, Anbury.) ... ... *Plasmodiophora Brassicae* Woron.

For foreign names see under Turnip and Swede.

Damping-off ... ... *Pythium de Baryanum* Hesse

White Blister (White Rust.) ... ... *Cystopus candidus* (Pers.) de Bary (= *Albugo candida* (Pers.) O. Kuntze)

For foreign names see under Turnip and Swede.

Downy Mildew ... ... *Peronospora parasitica* (Pers.) Tul.

SEAKALE (*Crambe*).

Black Rot ... ... *Pseudomonas campestris* (Pamm.) E. F. Sm.

For foreign names see under Cabbage, Cauliflower, etc.

Finger-and-Toe (Club Root, Anbury.) ... ... *Plasmodiophora Brassicae* Woron.

For foreign names see under Turnip and Swede.

Violet Root Rot... ... *Helicobasidium purpureum* (Tul.) Pat.
(Copper Web.) (*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

For foreign names see under Potato.

CUCUMBER (*Cucumis sativus*).

Mosaic ... ... Virus.

Mildew ... ... *Erysiphe Cichoracearum* DC.

Stem Rot ... ... *Didymella Lycopersici* Kleb. (*Diplodina Lycopersici* (Cooke) Hollós)

Anthracnose ... ... *Colletotrichum oligochaetum* Cav.
(2) anthracnose, (3) antracnosi, (4) Brennfleckenkrankheit, (5) fruchtvuur, (6) skiveplet.

Grey Mould ... ... *Botrytis cinerea* Pers.
For foreign names see under Cabbage, Cauliflower, etc.

Verticillium Wilt ... *Verticillium albo-atrum* Reinke & Berth.
(1) wilt, (3) verticilliosi, (4) Welkekrankheit, (5) verwelkungsziekte, (6) kransskimmel.

Gummosis ... ... *Cladosporium cucumerinum* Ell. & Arth.
(1) scab, (2) gommose, (3) gommosi, (4) Kratze, (5) fruktvuur, (6) gummiflod.

Blotch ... ... *Cercospora Melonis* Cooke
(3) ticchiolatura, (4) Blattbrand, (5) bladvuur, (6) rudeplet.

Fusarium Wilt ... ... *Fusarium* sp.
(3) avvizzimento, fusariosi, (4) Welkekrankheit, Trockenfäule, (5) verwelkungziekte, (6) slimskimmel.

VEGETABLE MARROW (*Cucurbita*).

Mildew ... ... *Erysiphe Cichoracearum* DC.

Grey Mould ... ... *Botrytis cinerea* Pers.
For foreign names see under Cabbage, Cauliflower, etc.

CARROT (*Daucus*).

Sclerotinia Rot ... ... *Sclerotinia Sclerotiorum* (Lib.) de Bary
(= *S. Libertiana* (Lib.) Fuck.)
(2) maladie des sclérotes, (3) mal dello sclerozio, marciume, (4) Sklerotienkrankheit, (5) sklerotienrot, (6) storknoldet baegersvamp.

Violet Root Rot ... *Helicobasidium purpureum* (Tul.) Pat.
(*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

For foreign names see under Potato.

CELERY (*Apium*).

Soft Rot ... ... *Bacillus carotovorus* L. R. Jones

For foreign names see under Onion.

Root Rot ... ... *Phoma apiicola* Kleb.

Leaf Spot (Blight.) ... ... *Septoria Apii* Chester
(=*S. Petroselini* Desm. var. *Apii* Bri. & Cav.)

(1) late blight, (2) rouille, (3) ticchiolatura delle foglie, (4) Blattfleckenkrankheit, (5) bladvlekkenziekte, (6) bladpletsyge.

PARSNIP (*Pastinaca*).

Soft Rot ... ... *Bacillus carotovorus* L. R. Jones

For foreign names see under Onion.

Mildew ... ... *Erysiphe Polygoni* DC.

Canker ... ... Non-parasitic.

ARTICHOKE (*Helianthus tuberosus*).

Sclerotinia Disease ... *Sclerotinia Sclerotiorum* (Lib.) de Bary
(= *S. Libertiana* (Lib.) Fuck.)

For foreign names see under Carrot.

LETTUCE (*Lactuca*).

Bacterial Spot ... ... *Bacterium pyocyaneum* (Gessard) Lehm. & Neum.
(= *B. marginale* N. A. Brown)

Downy Mildew ... ... *Bremia Lactucae* Regel

(2) meunier, (3) Peronospora, marciume, (4) falscher Mehltau, (5) valsche meeldauw, (6) salatskimmel.

Ring Spot ... ... *Marssonina panattoniana* Berl.

(1) anthracnose, (3) marciume, (4) Fäule.

Grey Mould ... ... *Botrytis cinerea* Pers.

For foreign names see under Cabbage, Cauliflower, etc.

SALSIFY (*Scorzonera*).

White Blister ... ... (White rust.) — *Cystopus cubicus* (Strauss) de Bary

Rust ... ... — *Puccinia hysterium* Röhl.

TOMATO (*Lycopersicum*).

Mosaic ... ... — Virus.

Stripe ... ... — *Bacillus Lathyri* Manns & Taubenh.

(4) Streifenkrankheit, (5) strepenziekte, (6) stregbakteriose. A virus disease with similar symptoms has been described in other countries.

Blight ... ... — *Phytophthora infestans* (Mont.) de Bary

Foot Rot and Damping-off — *Phytophthora cryptogea* Pethybr. & Laff. and *P. parasitica* Dast.

(2) fonte, (3) cancrena del pedale, (4) Keimlingskrankheit, (6) rodbrand.

Buck-Eye Rot ... ... — *Phytophthora parasitica* Dast. (= *P. terrestris* Sherb.)

Mouldy Fruit Rot ... — *Rhizopus stolonifer* (Ehrenb.) Lind (= *R. nigricans* Ehrenb.)

Stem Rot ... ... — *Didymella Lycopersici* Kleb. (*Diplodina Lycopersici* (Cooke) Hollós)

(4) Tomatenkrebs, Krebs, (6) koldbrand.

Sclerotinia Disease ... — *Sclerotinia Sclerotiorum* (Lib.) de Bary (= *S. Libertiana* (Lib.) Fuck.)

For foreign names see under Carrot.

Fruit Rot ... ... — *Phoma destructiva* Plowr. and *Didymella Lycopersici* Kleb.

(1) Phoma fruit rot, (5) Kanker (Didymella), (6) koldbrand (Didymella).

Leaf Spot ... ... — *Septoria Lycopersici* Speg.

Root Rot ... ... — *Colletotrichum atramentarium* (Berk. & Br.) Taubenh. (= *C. tabificum* Pethybr., *Vermicularia varians* Ducom.)

Grey Mould ... ... *Botrytis cinerea* Pers.

For foreign names see under Cabbage.

Verticillium Wilt ... *Verticillium albo-atrum* Reinke & Berth. and *V. Dahliae* Kleb.

For foreign names see under Cucumber.

Leaf Mould ... ... *Cladosporium fulvum* Cooke (Rust.)

(3) ticchiolatura, (4) Braunfleckenkrankheit, (5) bladziekte, (6) flöjlsplet.

Fusarium Wilt ... ... *Fusarium Lycopersici* Sacc.

(1) Wilt, (4) Fusarium-Welkekrankheit, (5) verwelkungsziekte, (6) Fusariumsovesyge.

Blossom End Rot ... Non-parasitic.

(5) neusrot, (6) griffelraad.

MINT (*Mentha*).

Rust ... ... *Puccinia Menthae* Pers.

BEET. (See Mangold, p. 152).

SPINACH (*Spinacia*).

Downy Mildew ... ... *Peronospora effusa* (Grev.) Rabenh.

FRUIT.

APPLE (*Pyrus Malus*).

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.

(2) galle en couronne, (3) rogna, tumori del colleto, tubercoli, (4) Kronengalle, Wurzelkropf, (5) wortelknobbels, (6) krongalle.

Phytophthora Rot ... *Phytophthora Cactorum* (Leb. & Cohn) Schroet. and *P. Syringae* Kleb.

Mildew ... ... *Podosphaera leucotricha* (Ell. & Everh.) Salm.

Blue Mould ... ... *Penicillium expansum* Thom

Canker and Eye Rot ... *Nectria galligena* Bres.

(1) European canker, (2) chancre, (3) cancro, (4) Krebs, (5) kanker, (6) kraeft.

Formerly incorrectly referred to *Nectria ditissima* Tul.

Coral Spot ... ... *Nectria cinnabarina* (Tode) Fr.

Bitter Rot ... ... *Glomerella cingulata* (Stonem.) Spauld. & v. Schrenk (*Gloeosporium fructigenum* Berk.)

Leaf Spot ... ... *Physalospora Cydoniae* Arn., *Phyllosticta* sp., etc.

Storage Fruit Spot ... *Pleospora pomorum* Horne, and other fungi.

Scab ... ... *Venturia inaequalis* Aderh. (Black Spot.) (*Fusicladium dendriticum* (Wallr.) Fuck.)

(2) tavelure, (3) ticchiolatura, (4) Schorf, (5) schurft, (6) skurv.

White Root Rot... ... *Rosellinia necatrix* (Hart.) Berl.

Blossom Wilt and Spur Canker ... *Sclerotinia cinerea* Schroet. (*Monilia cinerea* Bon.)

Brown Rot ... ... *Sclerotinia fructigena* Schroet. (*Monilia fructigena* Pers.)

(2) rot-brun, (3) marciume nero, (4) Braunfäule, (6) frugt-skimmel.

Silver Leaf ... ... *Stereum purpureum* Pers.

For foreign names see under Plum.

Root Rot ... ... *Armillaria mellea* (Vahl) Fr.

Die Back ... ... See under Plum.

Surface Canker ... ... *Myxosporium corticolum* Edgert.

Fly Speck ... ... *Leptothyrium Pomi* (Mont. & Fr.) Sacc.

Sooty Blotch ... ... Cause undetermined.

In the United States this disease is caused by *Gloeodes pomigena* (Schw.) Colby.

Rough Scab ... ... *Coniothecium chomatosporum* (Blister-Disease.) Corda

Bud Rot ... ... *Fusarium* sp.

Pink Rot... ... ... *Trichothecium roseum* Link (= *Cephalothecium roseum* Corda)

Bitter Pit ... ... Non-parasitic.
(1) stippen, (2) liège, points brun de la chair, (4) Stippflecke

Glassiness ... ... Non-parasitic.
(1) Water-Core, (4) Glasigwerden.

Leaf Scorch ... ... Non-parasitic.

PEAR (*Pyrus communis*).

Phytophthora Rot ... *Phytophthora Cactorum* (Leb. & Cohn) Schroet.

Leaf Blister ... ... *Taphrina bullata* (Berk.) Tul.

Mildew ... ... *Podosphaera leucotricha* (Ell. & Everh.) Salm.

Blue Mould ... ... *Penicillium expansum* Thom

Canker ... ... *Nectria galligena* Bres.
For foreign names see under Apple.

Coral Spot ... ... *Nectria cinnabarina* (Tode) Fr.

Leaf Fleck ... ... *Mycosphaerella sentina* (Fr.) Schroet.
(*Septoria piricola* Desm.)

Scab ... ... *Venturia pirina* Aderh.
(*Fusicladium pirinum* (Lib.) Fuck.)
For foreign names see under Apple.

White Root Rot... ... *Rosellinia necatrix* (Hart.) Berl.

Blossom Wilt ... ... *Sclerotinia cinerea* Schroet.
(*Monilia cinerea* Bon.)

Brown Rot ... ... *Sclerotinia fructigena* Schroet.
(*Monilia fructigena* Pers.)
For foreign names see under Apple.

Rust ... ... *Gymnosporangium* spp.

Silver Leaf ... ... *Stereum purpureum* Pers.
For foreign names see under Plum.

Root Rot ... ... *Armillaria mellea* (Vahl) Fr.

Bud Rot... ... ... *Fusarium fructigenum* Fr.

QUINCE (*Cydonia*).

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.
For foreign names see under Apple.

Mildew ... ... *Podosphaera leucotricha* (Ell. & Everh.) Salm.

Leaf Blight ... ... *Fabraea maculata* Atk. (*Entomosporium maculatum* Lév.)

The perfect stage of this fungus has not been found in Britain.

Brown Rot ... ... *Sclerotinia fructigena* Schroet.

For foreign names see under Apple.

Silver Leaf ... ... *Stereum purpureum* Pers.

For foreign names see under Plum.

MEDLAR (*Mespilus*).

Mildew ... ... *Podosphaera leucotricha* (Ell. & Everh.) Salm.

Leaf Blotch ... ... *Sclerotinia Mespili* Schellenb.

Rust ... ... *Gymnosporangium confusum* Plowr.

PLUM (*Prunus domestica*).

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.

For foreign names see under Apple.

Pocket Plums ... ... *Taphrina Pruni* (Fuck.) Tul. (= *Exoascus Pruni* Fuck.)

(1) plum pockets, (2) pochettes du prunier, (4) Taschen.

Witches' Brooms ... *Taphrina insititiae* (Sadeb.) Johans. (= *Exoascus insititiae* Sadeb.)

(2) balai de sorcière, (4) Hexenbesen, (5) heksenbezem.

Mildew ... ... *Podosphaera Oxyacanthae* (DC.) de Bary v. *tridactyla* (Wallr.) Salm.

Die Back ... ... Probably bacterial, but associated with *Diaporthe perniciosa* Marchal and *Cytospora* spp.

Branch Die Back ... *Cenangium Prunastri* (Pers.) Fr.

Occurs especially in Greengage.

Blossom Wilt, Spur Blight, Wither Tip and Brown Rot *Sclerotinia cinerea* Schroet. (*Monilia cinerea* Bon.)

Brown Rot ... ... *Sclerotinia fructigena* Schroet.

For foreign names see under Apple.

Rust ... ... *Puccinia Pruni-spinosae* Pers.

Silver Leaf ... ... *Stereum purpureum* Pers.

(2) plomb, (3) mal del piombo, (4) Milchglanz, (5) loodglans, (6) sølvglans.

Fomes Disease ... ... *Fomes pomaceus* (Pers.) Lloyd

Root Rot ... ... *Armillaria mellea* (Vahl) Fr.

Scab ... ... *Cladosporium carpophilum* Thuem.

Gummosis ... ... Various parasitic organisms; and non-parasitic.

CHERRY (*Prunus Cerasus*).

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.

For foreign names see under Apple.

Leaf Curl ... ... *Taphrina minor* Sadeb. (= *Exoascus minor* Sadeb.)

Witches' Brooms ... *Taphrina Cerasi* (Fuck.) Sadeb. (= *Exoascus Cerasi* Sadeb.)

(2) balai de sorcière, (4) Hexenbesen, (5) heksenbezem.

Leaf Scorch ... ... *Gnomonia erythrostoma* (Pers.) Auersw.

(4) Blattseuche.

Scab ... ... *Venturia Cerasi* Aderh. (*Fusicladium Cerasi* (Rabenh.) Sacc.)

Blossom Wilt and Brown Rot *Sclerotinia cinerea* Schroet. (*Monilia cinerea* Bon.)

Silver Leaf ... ... *Stereum purpureum* Pers.

For foreign names see under Plum.

Die Back ... ... See under Plum.

APRICOT (*Prunus Armeniaca*).

Die Back ... ... See under Plum.

Brown Rot ... ... *Sclerotinia fructigena* Schroet. and *S. cinerea* Schroet.

Silver Leaf ... ... *Stereum purpureum* Pers.

For foreign names see under Plum.

PEACH AND NECTARINE (*Prunus persica*).

Leaf Curl	*Taphrina deformans* (Berk.) Tul. (= *Exoascus deformans* Fuck.)

(2) cloque, (3) accartocciamento, bolla, (4) Kräusel, (5) krul, (6) blaeresyge.

Mildew	*Sphaerotheca pannosa* (Wallr.) Lév., var. *persicae* Woron.
Die Back	See under Plum.
Brown Rot	*Sclerotinia fructigena* Schroet. and *S. cinerea* Schroet.
Silver Leaf	*Stereum purpureum* Pers.

For foreign names see under Plum.

Fomes Disease	*Fomes pomaceus* (Pers.) Lloyd
Shot Hole	*Clasterosporium carpophilum* (Lév.) Aderh. (= *Coryneum Beijerinckii* Oud.)
Scab	*Cladosporium carpophilum* Thuem.

RASPBERRY (*Rubus Idaeus*).

Mosaic	Virus.
Crown Gall	*Bacterium tumefaciens* E. F. Sm. & Towns.

For foreign names see under Apple.

Anthracnose (Spot.)	*Plectodiscella veneta* Burkh. (*Gloeosporium venetum* Speg.)
Mildew	*Sphaerotheca Humuli* (DC.) Burr.
Spur Blight	*Didymella applanata* (Niessl) Sacc.
Rust	*Phragmidium Rubi-Idaei* (Pers.) Karst.
Blue Stripe Wilt ...	*Verticillium Dahliae* Kleb.

LOGANBERRY (*Rubus*).

Crown Gall	*Bacterium tumefaciens* E. F. Sm. & Towns.

For foreign names see under Apple.

Die Back	*Gnomonia Rubi* (Rehm) Wint.
Rust	*Phragmidium* (?) *violaceum* (Schultz) Wint.

STRAWBERRY (*Fragaria*).

Mildew	*Sphaerotheca Humuli* (DC.) Burr.
Leaf Spot	*Mycosphaerella Fragariae* (Tul.) Lindau (*Ramularia Tulasnei* Sacc.)
Leaf Scorch	*Marssonina Fragariae* (Sacc.) Kleb.

The perfect stage is *Diplocarpon Earliana* (Ell. & Everh.) Wolf = *Fabraea Fragariae* Kleb.

GOOSEBERRY (*Ribes Grossularia*).

American Mildew ...	*Sphaerotheca mors-uvae* (Schw.) Berk.
European Mildew ...	*Microsphaera Grossulariae* (Wallr.) Lév.
Coral Spot	*Nectria cinnabarina* (Tode) Fr.
Black Pustule	*Plowrightia ribesia* (Pers.) Sacc.
Leaf Spot	*Pseudopeziza Ribis* Kleb. (*Gloeosporium Ribis* (Lib.) Mont. & Desm.)
Cluster Cup Rust ...	*Puccinia Pringsheimiana* Kleb.
Root Rot	*Armillaria mellea* (Vahl) Fr.
Die Back	*Botrytis cinerea* Pers.

RED CURRANT (*Ribes rubrum*).

American Mildew ...	*Sphaerotheca mors-uvae* (Schw.) Berk.
European Mildew ...	*Microsphaera Grossulariae* (Wallr.) Lév.
Coral Spot	*Nectria cinnabarina* (Tode) Fr.
Black Pustule	*Plowrightia ribesia* (Pers.) Sacc.
Leaf Spot	*Pseudopeziza Ribis* Kleb. (*Gloeosporium Ribis* (Lib.) Mont. & Desm.)
Cluster Cup Rust ...	*Puccinia Pringsheimiana* Kleb.

Rust	*Cronartium ribicola* Dietr.
Root Rot	*Armillaria mellea* (Vahl) Fr.
Stem Toadstool	*Collybia velutipes* (Curt.) Fr.
Die Back	*Botrytis cinerea* Pers.
BLACK CURRANT (*Ribes nigrum*).	
Reversion	Virus.
American Mildew ...	*Sphaerotheca mors-uvae* (Schw.) Berk.
Coral Spot	*Nectria cinnabarina* (Tode) Fr.
Black Pustule	*Plowrightia ribesia* (Pers.) Sacc.
Leaf Spot	*Pseudopeziza Ribis* Kleb. (*Gloeosporium Ribis* (Lib.) Mont. & Desm.)
Cluster Cup Rust ...	*Puccinia Pringsheimiana* Kleb.
Rust	*Cronartium ribicola* Dietr.
Root Rot	*Armillaria mellea* (Vahl) Fr.
GRAPE VINE (*Vitis*).	
Crown Gall	*Bacterium tumefaciens* E. F. Sm. & Towns.
Downy Mildew ...	*Plasmopara viticola* (Berk. & Curt.) Berl. & de Toni
Mildew	*Uncinula necator* (Schw.) Burr. (*Oidium Tuckeri* Berk.)
Root Rot	*Armillaria mellea* (Vahl) Fr.
Anthracnose	*Gloeosporium ampelophagum* (Pass.) Sacc.
FIG (*Ficus*).	
Coral Spot	*Nectria cinnabarina* (Tode) Fr.
Canker	*Phomopsis cinerascens* (Sacc.) Trav.
Grey Mould and Die Back	*Botrytis cinerea* Pers.
MULBERRY (*Morus*).	
Blight	*Bacterium Mori* Boyer & Lamb.
Leaf Spot	*Septogloeum Mori* (Lév.) Bri. & Cav.

WALNUT (*Juglans*).

Bacterial Blight... ...	*Pseudomonas* (*Bacterium*) *Juglandis* Pierce
Blotch	*Gnomonia leptostyla* (Fr.) Ces. & de Not. (*Marssonina Juglandis* (Lib.) Magn.)

MELON (*Cucumis Melo*).

Mildew	*Erysiphe Cichoracearum* DC.
Grey Mould	*Botrytis cinerea* Pers.

For foreign names see under Cabbage, Cauliflower, etc.

ORNAMENTAL PLANTS.

ANEMONE.

Smut	*Urocystis Anemones* (Pers.) Wint.

(6) brand.

Cluster Cup Rust ...	*Puccinia Pruni-spinosae* Pers.

ARUM (*Richardia*).

Root Rot	*Phytophthora Richardiae* Buism.
Corm Rot ... ... (Soft Rot.)	*Bacillus Aroideae* Towns.

ASTER (*Callistephus*).

Foot Rot...	*Phytophthora cryptogea* Pethybr. & Laff.
Wilt	*Fusarium* spp.

CAMPANULA ... ...

Rust	*Coleosporium Campanulae* (Pers.) Lév.

CARNATION AND PINK (*Dianthus Caryophyllus*).

Rust	*Uromyces Dianthi* (Pers.) Niessl (= *U. caryophyllinus* (Schrank) Schroet.)
Leaf Rot...	*Pseudodiscosia Dianthi* Hösterm. & Laub.
Leaf Spot ... ... (4) Gelbfleckigkeit.	*Septoria Dianthi* Desm.
Ring Spot ... ... (Fairy Ring.)	*Heterosporium echinulatum* (Berk.) Cooke

(4) Nelkenschwärze, (6) heterosporiose.

Wilt ... ... *Fusarium culmorum* (W. G. Sm.) Sacc.
(Stem Rot, Foot Rot.)
(4) Stengelfäule.

CHRYSANTHEMUM (*C. indicum*).

Mildew ... ... *Oidium Chrysanthemi* Rabenh.

Rust ... ... *Puccinia Chrysanthemi* Roze

Blotch ... ... *Septoria chrysanthemella* Sacc.
(Leaf Spot.)

DELPHINIUM.

Black Blotch ... ... *Bacterium Delphinii* Bryan
(1) bacterial leaf spot, black spot, (2) bacteriose.

Mildew ... ... *Erysiphe Cichoracearum* DC.

HOLLYHOCK (*Althaea*).

Rust ... ... *Puccinia Malvacearum* Mont.

LAVENDER (*Lavandula*).

Scab ... ... *Phoma Lavandulae* Gab.

MICHAELMAS DAISY (*Aster*).

Mildew ... ... *Erysiphe Cichoracearum* DC.

Wilt ... ... *Verticillium Vilmorinii* Westerd. & van Luijk

PAEONY (*Paeonia*).

Blotch ... ... *Septoria Paeoniae* West.

Wilt ... ... *Botrytis Paeoniae* Oud.
(Rot.)
(5) botrytisziekte, (6) drueskimmel.

Grey Mould. ... ... *Botrytis cinerea* Pers.
For foreign names see under Cabbage, Cauliflower, etc.

PELARGONIUM.

Black Leg ... ... *Pythium* spp.
(1) stem rot, (4) Schwarzbeinigkeit.

Grey Mould ... ... *Botrytis cinerea* Pers.
(1) leaf spot, Botrytis blossom blight.
For other foreign names see under Cabbage, Cauliflower, etc.

ROSE (*Rosa*).

Crown Gall ... ... *Bacterium tumefaciens* E. F. Sm. & Towns.

For foreign names see under Apple.

Downy Mildew ... ... *Peronospora sparsa* Berk.
(Black Mildew.)

Mildew ... ... *Sphaerotheca pannosa* (Wallr.) Lév.

Black Spot ... ... *Diplocarpon Rosae* Wolf
(Blotch.) (*Actinonema Rosae* (Lib.) Fr.)

(1) leaf blotch, (2) taches noires, (4) Schwarzfleckigkeit, Schwarzfleckenkrankheit, (5) sterroetdauw, (6) straalesvamp, straaleplet.

The perfect stage of this fungus has not yet been recorded in Britain.

Leaf Scorch ... ... *Sphaerulina Rehmiana* Jaap (*Septoria Rosae* Desm.)

The perfect stage of this fungus has not yet been recorded in Britain.

Rust ... ... *Phragmidium mucronatum* (Pers.) Schlecht. (= *P. subcorticium* Wint.)

Stem Canker ... ... *Coniothyrium Fuckelii* Sacc.

(2) chancre, (4) Rosenkrebs.

Graft Disease ... ... *Coniothyrium Rosarum* Cooke & Harkn.

Grey Mould ... ... *Botrytis cinerea* Pers.

(2) moisissure grise, (6) drueskimmel.

SNAPDRAGON (*Antirrhinum*).

Shot Hole ... ... *Heteropatella Antirrhini* Budd. & Wakef. (*Cercosporella Antirrhini* Wakef.)

Stem Rot ... ... *Phyllosticta Antirrhini* Syd.
(Leaf Blotch, Leaf Spot.)

(1) Phyllosticta blight.

SWEET PEA (*Lathyrus*).

Streak ... ... *Bacillus Lathyri* Manns & Taubenh.

Mildew ... ... *Erysiphe Polygoni* DC.

White Mould ... ... *Erostrotheca multiformis* Martin & Charles (*Cladosporium album* Dows.)

(1) White Blight.

The perfect stage of this fungus has not been found in Britain.

SWEET WILLIAM (*Dianthus barbatus*).

Rust ... ... *Puccinia Lychnidearum* Link f. *Dianthi* Grove

Leaf Spot ... ... *Heterosporium echinulatum* (Berk.) Cooke

VIOLA and PANSY (*Viola*).

Mildew ... ... *Oidium* sp.

Rust ... ... *Puccinia aegra* Grove

Leaf Spot ... ... *Ascochyta Violae* Sacc. & Speg. and *Ramularia agrestis* Sacc.

White Spot ... ... *Ramularia lactea* (Desm.) Sacc.

(4) Weissfleckenkrankheit, (5) bladvlekkenziekte.

VIOLET (*Viola odorata*).

Smut ... ... *Urocystis Violae* (Sow.) Fisch. v. Waldh.

(4) Schwielbrand, (5) stengelbrand, (6) brand.

Rust ... ... *Puccinia Violae* (Schum.) DC.

Leaf Spot ... ... *Septoria Violae* West. and *Ascochyta Violae* Sacc. & Speg.

White Spot ... ... *Ramularia lactea* (Desm.) Sacc.

WALLFLOWER (*Cheiranthus*).

Finger-and-Toe ... ... *Plasmodiophora Brassicae* Woron.
(Club Root, Anbury.)

For foreign names see under Turnip and Swede.

Downy Mildew ... ... *Peronospora parasitica* (Pers.) Tul.

Grey Mould ... ... *Botrytis cinerea* Pers.

For foreign names see under Cabbage, Cauliflower, etc.

ALMOND (*Amygdalus*).

Leaf Curl ... ... *Taphrina deformans* (Berk.) Tul. (= *Exoasous deformans* Fuck.)

For foreign names see under Peach.

Silver Leaf ... ... *Stereum purpureum* Pers.

For foreign names see under Plum.

AZALEA.

Gall ... ... *Exobasidium Vaccinii* (Fuck.) Woron.

(2) galles foliaires, (4) Exobasidiumkrankheit.

Leaf Scorch ... ... *Septoria Azaleae* Vogl.

LILAC (*Syringa*).

Leaf Blotch ... ... *Heterosporium Syringae* Kleb.

RHODODENDRON.

Die Back ... ... *Stereum purpureum* Pers.

Leaf Scorch ... ... *Sporocybe Azaleae* (Peck) Sacc.

HYACINTH (*Hyacinthus*).

Yellow Disease ... ... *Bacterium Hyacinthi* Wakk.

(4) gelber Rotz, (5) geelziek.

Soft Rot ... ... *Bacillus carotovorus* L. R. Jones

Black Slime ... ... *Sclerotinia bulborum* (Wakk.) Rehm

(4) Schwarzer Rotz, (5) zwart snot.

Stalk Break ... ... Non-parasitic.

(4) Abstossen, (5) uitwerpen.

TULIP (*Tulipa*).

Shanking ... ... *Phytophthora cryptogea* Pethybr. & Laff.

Fire ... ... *Botrytis Tulipae* (Lib.) Lind

(Tulip mould.) ... (= *B. parasitica* Cav.)

(1) Botrytis blight, (4) Botrytiskrankheit, (5) vuur.

Grey Bulb Rot ... ... *Sclerotium Tuliparum* Kleb.

(4) Sklerotienkrankheit, (5) wegblijven.

Whetzel and Arthur have recently transferred this fungus to the genus *Rhizoctonia*.

Topple ... ... (Wet Stem.)	Non-parasitic.

(4) Umfallen, Knickerkrankheit, (5) keepen.

NARCISSUS.

Leaf Scorch	*Stagonospora Curtisii* (Berk.) Sacc. (= *S. Narcissi* Hollós)
Smoulder ... ... (5) smeul.	*Botrytis narcissicola* Kleb.
Fire	*Botrytis polyblastis* Dows.
White Mould	*Ramularia Vallisumbrosae* Cav.

SNOWDROP (*Galanthus*).

Grey Mould	*Botrytis galanthina* (Berk. & Br.) Sacc.

LILY (*Lilium*).

Rosette ... ... (1) Yellow Flat.	Virus.
Rust	*Uromyces Lilii* (Link) Fuck. (= *U. Erythronii* DC.)
Lily Disease	*Botrytis elliptica* (Berk.) Cooke

GLADIOLUS.

Scab and Neck Rot ...	*Bacterium marginatum* McCulloch
Storage Rot	*Penicillium Gladioli* McCulloch & Thom
Smut	*Urocystis Gladioli* (Requien) W. G. Sm.
Hard Rot and Leaf Spot (4) Hartfäule.	*Septoria Gladioli* Pass.
Dry Rot ... ... (5) zwartevlekkenziekte.	*Sclerotium Gladioli* Massey

CROCUS.

Copper Web ... ... (2) la mort.	*Helicobasidium purpureum* (Tul.) Pat. (*Rhizoctonia Crocorum* (Pers.) DC. and *R. violacea* Tul.)

IRIS.

Soft Rot	*Bacillus omnivorus* van Hall, *Pseudomonas Iridis* van Hall, etc.

(3) batteriosi, (5) rottingsziekte.

Rust ... ... *Puccinia Iridis* (DC.) Wallr.

Leaf Spot ... ... *Heterosporium gracile* Sacc.

Two species of *Didymellina* have been said to be the perfect stage of this fungus, viz. *D. Iridis* (Desm.) v. Hoehn. and *D. macrospora* Kleb.; the second is probably correct.

MISCELLANEOUS.

FLAX (*Linum*).

Rust ... ... *Melampsora Lini* (Pers.) Desm.

Seedling Blight ... ... *Colletotrichum Lini* (Westerd.) Toch.
(= *C. linicolum* Pethybr. & Laff.)

(5) regenvlek.

Browning and Stem-Break *Polyspora Lini* Laff.

Grey Mould ... ... *Botrytis cinerea* Pers.

For foreign names see under Cabbage, Cauliflower, etc.

Wilt ... ... *Fusarium Lini* Bolley

(2) flétrissement, (3) avvizzimento, (4) Welke, Leinmüdigkeit, (6) slimskimmel.

HOP (*Humulus*).

Mosaic ... ... Virus.

(3) virescenza.

Nettlehead ... ... Cause unknown.

Crown Gall ... *Bacterium tumefaciens* E. F. Sm. & Towns.

Downy Mildew ... ... *Pseudoperonospora Humuli* (Miyabe & Tak.) G. W. Wilson
(= *Peronoplasmopara Humuli* Miyabe & Tak.)

Mildew ... ... *Sphaerotheca Humuli* (DC.)Burr.
(Mould, Red Mould.)

Leaf Spot ... ... *Cercospora cantuariensis* Salm. & Worm.

Canker ... ... *Fusarium* sp.

(2) chancre, (3) fusariosi, (6) slimskimmel.

TOBACCO (*Nicotiana*).

Mosaic ... ... Virus.

Root Rot ... ... *Thielavia basicola* Zopf[1]

(1) black root rot, (3) marciume radicale, (4) Wurzelfäule, (6) rodbrand.

RHUBARB (*Rheum*). ...

Crown Rot ... ... *Bacterium Rhaponticum* Millard

(3) marciume, (4) Wurzelhalsfäule.

Rust ... ... *Puccinia Phragmitis* (Schum.) Koern.

MUSHROOM (*Psalliota*).

Brown Blotch ... ... *Pseudomonas Tolaasi* S. G. Paine

(3) batteriosi, (4) Braunfleckigkeit.

White Mould ... ... *Mycogone perniciosa* Magn.

(2) môle, (3) deformazione parassitaria, (4) Weissschimmel.

LIST OF AUTHORS' NAMES AND ABBREVIATIONS.

Aderh.	R. Aderhold, 1865–1907.
Appel	O. Appel.
Arn.	G. Arnaud.
Arth.	J. C. Arthur.
Atk.	G. F. Atkinson, 1854–1918.
Auersw.	B. Auerswald, 1818–70.
Bayl. Elliott	J. S. Bayliss Elliott.
Beeley	F. Beeley.
Berk.	M. J. Berkeley, 1803–89.
Berl.	A. N. Berlese, 1864–1903.
Berth.	G.D.W. Berthold, 1854– .
Biv.-Bern.	A. de Bivona-Bernardi, 1778–1834.
Bjerk.	C. Bjerkander, 1735–95.
Blox.	A. Bloxam, 1801–78.
Bolley	H. L. Bolley.
Bon.	H. F. Bonorden, 1801– .
Bourd.	H. Bourdot.
Boyer	G. Boyer.
Br.	C. E. Broome, 1812–86.
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Bri.	G. Briosi, 1846–1920.
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Bryan	Mary K. Bryan.
Budd.	W. Buddin.
Buism.	Christine Buisman.
Burkh.	W. H. Burkholder.
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Colby	A. S. Colby.
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DC.	Aug. Pyr. de Candolle, 1778–1841.
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de Not.	G. de Notaris, 1805–77.
Desm.	J. B. H. J. Desmazières, 1787–1862.
de Toni	G. B. de Toni, 1864–1924.
Dietr.	H. A. Dietrich.
Dows.	W. J. Dowson.
Drechsl.	C. Drechsler.
Ducom.	V. Ducomet.
Edgert.	C. W. Edgerton.
Eds.	H. A. Edson.
Ehrenb.	C. G. Ehrenberg, 1795–1876.
Eid.	M. E. E. Eidam, 1845–1901.

[1] The conidial stage, *Thielaviopsis basicola* (Berk.) Ferraris is that commonly found in Britain. Recent work indicates that this is a distinct fungus.

Ell. J. B. Ellis, 1829–1905.
Ch. Elliott Charlotte Elliott.
Eriksss. J. Eriksson.
Everh. B. M. Everhart, 1818–1904.
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Fitz. H. M. Fitzpatrick.
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Frost C. C. Frost, 1805–1880.
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Gab. L. Gabotto.
Galz. A. Galzin, 1853–1925.
Gessard C. Gessard.
Grev. R. K. Greville, 1794–1866.
Grove W. B. Grove.
Güss. H. T. Güssow.
Harkn. H. W. Harkness, 1821– .
Hart. R. Hartig, 1839–1901.
Harz C. O. Harz.
Hedw. f. R. A. Hedwig, 1772–1806.
Henn. Ernst Henning.
Hesse R. Hesse, 1844–1912.
Hollós L. Hollós.
Horne A. S. Horne.
Hösterm. G. Höstermann.
Jaap O. Jaap, 1864–1922.
Jens. J. L. Jensen, 1836–1904.
Johans. C. J. Johanson, 1858–88.
L. R. Jones L. R. Jones.
Karak. B. P. Karakulin.
Karst. P. A. Karsten, 1834–1917.
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O. Kuntze Otto Kuntze, 1843–1907.
G. Kunze Gustav Kunze, 1793–1851.
Laff. H. A. Lafferty.
Lagerh. G. von Lagerheim, 1860–1926.
Lamb. F. Lambert.
Laub. R. Laubert.
Leb. H. Lebert, 1813–78.
Lehm. K. B. Lehmann.
Lév. J. H. Léveillé, 1796–1870.
Lib. Marie Anne Libert, 1782–1865.
Lind Jens Lind.
Lindau G. Lindau, 1866–1923.
Link H. F. Link, 1767–1851.
Liro J. I. Liro (formerly Lindroth).
Lloyd C. G. Lloyd, 1859–1926.
Magn. P. Magnus, 1844–1914.
Manns T. F. Manns.
Marchal El. and Em. Marchal.
Martin G. H. Martin.
Massey L. M. Massey.
McCulloch Lucia McCulloch.
Melh. I. E. Melhus.
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Miyabe K. Miyabe.
Mont. J. F. C. Montagne, 1784–1866.
Munn M. T. Munn
Neum. R. Neumann, 1884–1910.
Niels. P. Nielsen, 1829– .
Niessl G. von Niessl, 1839–1919.
Otth G. H. Otth, 1806–74.
Oud. C. A. J. A. Oudemans, 1825–1906.
Owen M. Nest Owen.
Paine S. G. Paine.
Pamm. L. H. Pammel.
Pass. G. Passerini, 1816–93.
Pat. N. Patouillard, 1854–1926.
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Pers. C. H. Persoon, 1755–1837.
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Rehm H. Rehm, 1829–1916.
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Roze E. Roze, 1833–1900.
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Sadeb. R. E. B. Sadebeck, 1839–1905.
Salm. E. S. Salmon.
Schellenb. H. C. Schellenberg, 1872–1923.
Schilb. K. Schilberszky.
Schlecht. D. F. L. von Schlechtendal, 1794–1866.
Schm. J. K. Schmidt, 1793–1850.
Schrank F. von P. von Schrank, 1747–1835.
Schroet. J. Schroeter, 1835–94.
Schultz C. F. Schultz, 1765–1837.
E. S. Schultz E. S. Schultz.
Schum. H. C. F. Schumacher, 1757–1830.
Schw. L. D. von Schweinitz, 1780–1834.
Sherb. C. D. Sherbakoff.
E. F. Sm. Erwin F. Smith, 1854–1927.

W. G. Sm.	Worthington G. Smith, 1835–1917.
Sow.	James Sowerby, 1757–1822.
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Speg.	C. Spegazzini, 1858–1926.
Stansf.	O. P. Stansfield.
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Strauss	F. C. J. von Strauss, 1787–1855.
Swing.	W. T. Swingle.
Syd.	H. Sydow.
Tak.	Y. Takahashi.
Taubenh.	J. J. Taubenhaus.
Thaxt.	R. Thaxter.
Thom	C. Thom.
Thuem.	F. K. A. von Thuemen, 1839–92.
Toch.	Y. Tochinai.
Tode	H. J. Tode, 1733–97.
Towns.	C. O. Townsend.
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Trel.	W. Trelease
Tul.	L. R. Tulasne, 1815–85. C. Tulasne, 1816–84.
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Vahl	M. H. Vahl, 1749–1804.
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Wakef.	E. M. Wakefield.
Wakk.	J. H. Wakker.
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Wallr.	C. F. W. Wallroth, 1792–1857.
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Westerd.	Johanna Westerdijk.
Wille	J. N. F. Wille, 1858–1924.
G. W. Wilson	Guy West Wilson.
Wint.	G. Winter, 1848–87.
Wolf	F. A. Wolf.
Worm.	H. Wormald.
Woron.	M. S. Woronin, 1838–1903.
Zopf	F. W. Zopf, 1846–1909.

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REVIEW.

Hyménomycètes de France (*Hetérobasidiés-Homobasidiés gymnocarpes*). By H. BOURDOT and A. GALZIN. Pp. iv, 761; 185 figs. in text. Paris: P. Lechevalier, 1928. Frs. 150.

During the past twenty-five years our knowledge of the lower Basidiomycetes has made enormous strides. The Abbé Bresadola, with his careful and accurate descriptions of microscopic characters, broke new ground in the study of these forms. He has been followed by others, notably by von Hoehnel and Litschauer in Austria, by Burt and Overholts in America, and by Bourdot in France. The series of monographs prepared by the Abbé Bourdot in conjunction with the late M. A. Galzin, which began in 1909 and have continued to the present day, have been long regarded as indispensable for the determination of European Heterobasidieae, Thelephoraceae, Hydnaceae, etc. The earlier papers have necessarily become out of date with increasing knowledge. Hence the announcement that a revised edition, in book form, of the *Hyménomycètes de France* was in preparation was welcome news to all those interested in these groups.

The present volume, published under the auspices of the Société Mycologique de France, is a wonderful record of many years' work by M. Galzin, the

indefatigable collector, and the Abbé Bourdot, to whom all his collections were sent.

Bourdot and Galzin follow in its broad lines the classification proposed by Patouillard in his *Essai taxonomique*, and the present volume includes the "Basidiomycètes hetérobasidiés," with the sections Exobasidiaceae and Aphyllophoraceae of the "Basidiomycètes homobasidiés" of that arrangement; that is, all Hymenomycetes other than the Agaricaceae.

The extraordinary progress which has been made in recent years in the study of species is revealed by examination of the numbers included in certain genera. For instance, under *Corticium* and *Gloeocystidium* are enumerated no less than 165 species and sub-species, and under *Peniophora* 102, as against 99 and 66 respectively in the earlier papers of 1911 and 1912. Even more startling is the list of 53 species of *Hypochnus* (here called *Tomentella*). There is moreover no question that most of Bourdot's new species are well-founded and recognisable by other workers. It is interesting to compare these figures with the species recorded for Britain. In Rea's *British Basidiomycetae* and *Supplement* the numbers are: *Corticium* (including *Gloeocystidium*), 48; *Peniophora*, 31; *Hypochnus*, 21. As it is probable that many of the Continental forms occur also in this country, it is obvious that there is still room for much valuable work by those who are willing to give the time and patience necessary for collecting these lowly forms.

Keys are provided for the determination of genera and species. Perhaps from considerations of space, the authors have adopted the numerical form of key, as used by Burt in his *Thelephoraceae of North America*. This is much less convenient in use than the more natural form used in the earlier papers in the *Bull. Soc. Myc. France*, and it is unfortunate that this earlier form could not have been retained.

Each species is given a careful and detailed description, supplemented frequently by valuable ecological notes based on field observations. In many cases small text-figures, showing the principal microscopic characters, have been added.

It is inevitable that followers of the International Rules of Nomenclature and of the Type-basis Code should differ from the school of Patouillard in such matters as the use of *Phylacteria* for *Thelephora* and *Tomentella* for *Hypochnus*. Apart from such matters of opinion, however, one can find little to criticise in the work under review. It will undoubtedly rank as one of the classics of taxonomic literature.

The work is printed in clear type in a large 8vo form, and is provided with a complete index of the families, genera and species dealt with, with their synonyms. The price is moderate for a book of this class.

E. M. W.

PROCEEDINGS, 1928.

PHYTOPATHOLOGICAL MEETING. EXPERIMENTAL AND RESEARCH STATION, CHESHUNT, HERTS. *5th May.*

AUTUMN FORAY AND ANNUAL MEETING. LITTLEHAMPTON. *1st–6th October.*

2nd Oct. Presidential Address. Prof. Dame H. C. I. GWYNNE-VAUGHAN, D.Sc., LL.D. Problems of Development in the Fungi.

3rd Oct. Dr A. SMITH and Mr W. C. MOORE. Recent Aspects of Plant Diseases.

4th Oct. Col. C. T. GREEN, A.M.S. Popular Talk on British Fungi illustrated by Coloured Lantern Slides.

5th Oct. Mr J. Ramsbottom. Fairy Rings.
Mr Carleton Rea. Commentary on specimens during the Foray.

AUTUMN FORAY WITH ESSEX FIELD CLUB. EPPING FOREST. *13th Oct.*

AUTUMN FORAY FOR LONDON STUDENTS. WIMBLEDON COMMON. *20th Oct.*

AUTUMN FORAY WITH BRITISH ECOLOGICAL SOCIETY. BURNHAM BEECHES. *27th Oct.*

MEETING. UNIVERSITY COLLEGE, LONDON. *17th Nov.*

B. BARNES. The Production of Variations in *Botrytis cinerea* by heating the spores.

W. R. I. COOK. A new *Sorosphaera.*

R. PAULSON. The interpretation of the microscopic images of *Xanthoria parietina.*

E. M. WAKEFIELD and W. BUDDIN. The Fungus causing Carnation leaf rot.

S. P. WILTSHIRE. A *Stemphylium* saltant of an *Alternaria.*

E. BARTON WRIGHT. The biochemistry of wood affected by *Merulius lacrymans.*